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Cytology and Genetics of Barley..... LUTHER SMITH 133

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THE BOTANICAL REVIEW

VOL. XVII MARCH, 1951 NO. 3

# GENETICS AND CYTOLOGY OF BARLEY

*(Continued from January issue)*

LUTHER SMITH

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## GENETIC STUDIES

Barley is one of the half dozen most thoroughly genetically analyzed species of plants. There are a number of reasons why barley is in this select group, but the chief ones are probably these: *a*) the wide distribution of the barley plant; *b*) the smaller number of chromosomes; *c*) the almost complete self-fertilization and yet relative ease of artificial hybridization; and *d*) the wealth of easily classifiable hereditary characters. It has already become apparent in this review that barley breeders and geneticists have been blessed with a multitude of genetic forms, so that it has been possible to study the genetics of a large number of characters whose segregations were clear-cut. The thousands of X-ray-induced mutants have only added to the already great abundance of spontaneous mutants. No student, teacher or research worker interested in barley genetics need lack for material to study.

Tschermak (831) was studying inheritance in barley, as well as in wheat, oats and rye, when he rediscovered Mendel's monumental laws of heredity. Rimpau (656, 657, 658) and Liebscher (493), among others, had earlier noted the dominance or partial dominance of a number of characters in barley and the reappearance of recessives in later generations, but failed to analyze the observations mathematically. Additional information on the early studies in barley genetics may be found in papers by Blaringhem (1910A), Rimpau (659), Schiemann (695) and Tschermak (831, 832). A number of later publications are notable for their treatments of genetic studies in barley (24, 115, 146, 276, 320, 338, 340, 373, 399, 462, 464, 518, 660, 672, 676, 677, 837, 901) or for citations to literature on the subject (778, 873). Special attention is called to the relatively recent papers of Isenbeck and Hoffman (399) Robertson and co-workers (676, 677) and Nagao and Takahashi (1946A) for their intensive treatments of genetic studies in barley and for their extensive bibliographies.

The phenotypes and genetic bases of many characters in barley have been reported by numerous workers with remarkable unanimity. The same cannot be said for symbols to label the genes for these characters. An effort has been made by barley geneticists, particularly D. W. Robertson and G. A. Wiebe, to establish a uniform system of gene symbols through a Committee on Nomenclature. Because of the confusion that might arise if the original author's gene symbols were given in this review, and the difficulty of changing these symbols to those recommended by the Committee on Nomenclature (676, 677), as well as the fact that the Committee has not yet designated a number of reported genes by approved symbols, it was deemed wise in most cases to discuss the genetics of various characters without the use of any symbols.

An effort has been made to list alphabetically the characters that have been studied genetically. In many cases, of course, particular characters have been called by several names, so a choice had to be made. Many of the characters were described and illustrated by Aberg and Wiebe (11). The characters are given numbers for cross references with Table 3. After the character name there are given, where possible, the approved gene symbol(s) and the linkage group(s) in which the gene(s) has (have) been reported to be.

## Types of Genetic Characters

### COLOR VARIANTS—OTHER THAN CHLOROPHYLL.

*Chaff Colors*

Lewicki (489) made a valuable contribution to the knowledge of pigments in chaff and seeds of barley. Four ear colors were distinguished: *a*) white or yellow; *b*) black without anthocyanin; *c*) black with much anthocyanin, some of which remained at maturity; *d*) black with much anthocyanin in immature stages only. Four colors of seeds were also distinguished: *a*) yellow; *b*) green (like rye); *c*) violet (various shades); *d*) blackish-brown. The pigments for the colors were studied histologically and biochemically.

Buckley (115), Bauman (52) and others have distinguished colors other than those mentioned above. According to Buckley (115), a red pericarp and blue aleurone give a purple color, and black seeds are caused by a melanin-like pigment in the pericarp.

In addition to self-colored lemmas, there are also types in which only the veins are colored (115).

Kondo and co-workers (444, 445), using phenol solutions, were able to produce various shades of brown in the pericarp from almost colorless to blackish-brown. The coloration depended upon the variety of barley or wheat, temperature and maturity of the seed. The genetics of the color reaction was not studied, but, since it varied among varieties, it was possibly a heritable character. A somewhat similar result was obtained by Gudkov (279) with a 15% solution of HCl. The solution developed color in unripe seeds of varieties that normally have color when ripe, but not in white or yellow varieties.

For further information and a concise bibliography on pigmentation in barley, the reader is referred to the recent study of Takahashi and Yamamoto (1950aA). (See also Grain Colors.)

(1) Black Chaff Color (B, $B^{mb}$, $B^{g}$, b—2).

Black "glume" color is one of the characters that a large number of workers have studied, about which there is almost complete agreement as to its genetic basis. Black is dominant to non-black and segregates in a 3 : 1 ratio in many crosses (42, 65, 66, 68, 107, 115, 146, 225, 233, 275, 276, 308, 342, 434, 461, 479, 521, 522, 532, 638, 657, 658, 660, 672, 716, 831, 838, 842, 844, 868).

Woodward (896, 897) found evidence of an allelomorphic series of three genes for degree of black pigmentation of lemma and pericarp: black, gray and white. In each combination the darker color was dominant over the lighter and segregated monofactorially. Regel (649) reported evidence for two cases of spontaneous mutation from black to white chaff. In the same article it was pointed out that the degree of pigmentation could be altered in some varieties by selection. Black in the glumes and pericarp appears to be conditioned by the same gene (146, 372).

Tschermak (837) crossed a black-chaffed variety with a purple-chaffed variety and obtained in $F_2$, 12 black: 3 purple: 1 white, indicating digenic inheritance with black dominant to purple and purple dominant to white.

(2) Brownish-Yellow Chaff Color.

Brownish-yellow chaff color was found (676, 794) to be caused by a single gene which was dominant to white and linked (38.5% recombination) with the factor for two rows (Group 1). It was suggested (676) that this factor is the same as the factor for orange lemma, but the latter factor is a recessive.

(3) Orange Chaff Color (o—5).

Orange chaff is caused by a single gene which is recessive to the factor for white chaff (52, 115, 373, 565).

(4) Purple Chaff Color (P—1; P2— ; P3— ).

Purple chaff color is dominant to white, but more than one genic basis has been found for the character. Several workers have reported that the character is conditioned by one gene pair (68, 225, 373). Miyake and Imai (543) thought the purple color was caused by two incompletely dominant genes with additive effects. There was also considerable variation in expression, probably from environmental factors. Buckley (115) found purple to be inherited as a single-factor dominant in some crosses, but in other cases two complementary genes, when dominant, inhibited the gene for purple lemma. Waddoups (868) observed a 3: 1 ratio in the $F_2$ of a cross between purple- and white-chaffed parents, but one cross between two white-chaffed parents gave a 9: 7 ratio of purple to white in $F_2$. So et al. (737) reported 9: 7,

15:1, and 1:2:1 ratios for deep purple, light purple and colorless in different crosses.

(5) Purple Veins in Lemma ($P_e$—1; $P_e$— ; $P_f$— ).

According to Buckley (115), purple veins in the lemma are determined by three dominant gene pairs.

(6) Red Chaff Color.

Red chaff color was reported by Kezer and Boyak (434) to be conditioned by a single dominant gene.

*Grain Colors*

Harlan (310, 311) reported that two pigments were responsible for seed colors in barley: *a*) anthocyanin, violet in acid and blue in alkaline solution; and *b*) a melanin-like black pigment. These pigments may occur in the hulls, pericarp, aleurone layer and occasionally deeper in the endosperm. If neither pigment is present, seeds are white. If anthocyanin is present in the pericarp only, seeds are violet; and if it is present only in the aleurone layer, seeds appear blue. Anthocyanin in an acid condition in the pericarp and in an alkaline condition in the aleurone results in a purple color.

It will be noted in the succeeding paragraphs that more grain colors have been studied than were described by Harlan (310) or Lewicki (489). Some of these can probably be accounted for by assuming that some investigators gave the same genotypes different phenotype names. Violet, black-brown, green, yellow and yellow-green kernels were illustrated in color by Aberg (6, plate 20). A number of chaff and seed colors were also published by Wiggans (891).

(7) Black Pericarp Color.

Biffen (68) and Buckley (115) reported that black color in the hulls was associated with color in the grain which was localized in the pericarp (115). However, in a footnote Biffen pointed out that in *H. himalayense* colored grains were enclosed in nearly colorless chaff. Ubisch (844) was unable to decide whether black chaff and black pericarp were caused by the same gene or not. In crosses between black- and white-grained (and chaffed) types,

black grain color was dominant and segregated in approximately a 3:1 ratio in $F_2$. Black was also dominant to red pericarp (115, 373).

Kajanus and Berg (420) reported that violet-brown seed color was the result of two gene pairs—one for blue aleurone and the other for brown pericarp. The two dominants together produced a violet-brown; when both were recessive, the seed was yellow. Whether or not this "brown pericarp" is the same as "black pericarp" was not stated.

Other studies on the genetics of black grain and chaff color (135–137) in a cross between a common, white, rough-awned variety and a black, smooth-awned variety (according to the writers, probably a variety of *H. ciorhyncum* from Algiers) produced odd results. Seeds on $F_1$ plants were black, but in $F_2$ the segregation was approximately 2 black : 1 white (135). However, apparently the writers thought that there were different kinds of spikes, with respect to both color and barbs on the awns, on the $F_1$ plants; so possibly conditions were not favorable for development of pigment, and the results may not have been too reliable.

Tschermak (838) crossed black- with yellow-seeded types and in $F_2$ obtained black, purple tinged with green, yellowish-green and yellow segregates. Presumably the colors resulted from pigments in the pericarp. Purple × yellow produced $F_2$ plants with purple, purple tinged with green, yellowish-green and yellow seeds. Savinskaja (692) also obtained purple-seeded $F_2$ plants in crosses between black- and white-seeded plants. Of 78 $F_2$ plants, 62 had black; ten had white; and six had purple seeds.

From the foregoing review of work on the genetics of black pericarp color, it is evident that the results lack uniformity. Probably most of the difficulty stems from the fact that a careful distinction was not always made between glume and pericarp colors. The results would probably have been more clear-cut if naked varieties had been regularly used. This was done by Smith (723) who distinguished four seed (pericarp) colors. Raisin-black was dominant to pinkish-buff, giving in the $F_2$ 9 raisin-black : 3 hazel : 3 cinnamon-buff : 1 pinkish-buff. Raisin-black × hazel gave 3 raisin-black : 1 hazel $F_2$ plants. Hazel × pinkish-buff gave 3 hazel : 1 pinkish-buff $F_2$ plants. These observations

may belong under the discussion of red pericarp below, since symbols Re and $Re_1$ were suggested for the genes involved.

(8) Blue Aleurone (B1—4; B12—3).

Most of the reports indicate that blue aleurone is caused by a single dominant gene (115, 308, 373, 420, 461, 543, 672, 735). Myler and Stanford (565) obtained a 3:1 segregation for blue aleurone in the $F_2$ of some crosses; but obtained a 9:7 ratio in the $F_2$ of a cross between two white varieties—indicating the presence of two complementary factors. So and Imai (735) studied the same cross reported by Miyazawa (544), but came to quite different conclusions which fit the present concept of inheritance of blue vs. white seed color. Since the blue color is in the aleurone, xenia may be observed when the cross is made on the white-seeded parent. However, expression of the character is frequently influenced by environment.

Kuckuck (461) noted that the genes for black chaff color and bluish-black aleurone not only were different genes but were unlinked.

(9) Purple Pericarp Color (P—1).

Only a few workers have studied the genetics of purple pericarp, but they seem to agree that purple is dominant to white or yellow and produced by a single gene (146, 565, 844).

(10) Red Pericarp Color (Re—5; Re2—1; J— ; J2— ).

Red has been reported to be dominant to white pericarp and caused by one gene in some crosses (115, 146), by two genes in others (115). Red is recessive to black pericarp (115, 373). The difference between black and red was conditioned by two genes in some crosses, and in other crosses by two additional complementary factors that affected the expression of the two primary genes (115). Robertson [11], in crossing two red types, obtained a purple $F_1$ which segregated in $F_2$, "proving the complementary-factor hypothesis".

Greenish-brown vs. yellow seed color was reported to result from a single factor difference (48).

Fraser (225) noted that colored seed was dominant to color-

[11] Unpublished observations.

less, without specifying the colors involved or segregation ratios. (See Chaff Colors.)

*Plant Colors*

(11) Auricle Color.

Presence and absence of red pigment in the auricle was found to segregate in 3:1 and 10:6 ratios in different crosses (372). It was assumed that one gene was mainly responsible for formation of anthocyanin in the auricle, but this gene did not express itself except in the heterozygous condition, unless the other, intensifier gene, was also present in the dominant condition. Ubisch (844) observed that red color in the auricle, nodes and other places was dominant. Gassner and Straib (1937A) observed that a deficiency of N or a higher concentration of $CO_2$ increased anthocyanin development, but that K or P by themselves were relatively ineffective in changing the concentration of the pigment.

(12) Purple Straw (Pr—1).

In a cross studied by Robertson (663), purple straw was monofactorially determined.

(13) Red Stem (Rs—3).

Briggs and Stanford (101) reported red stem color to be determined by a single gene pair in one cross.

COLOR VARIANTS—CHLOROPHYLL.

*Types*

Almost every conceivable type of cholorophyll variation has been observed, particularly among the mutants resulting from X-radiation. This statement is based on personal observations on over 1,000 chlorophyll mutants (731a and unpublished observations) and on the reports of Stadler (742–745) and Gustafsson (285, 297) covering probably another 1,000 each. The most frequent chlorophyll mutant is white, followed in frequency by yellow-green, virescent, yellow, transversely zoned (various types) and longitudinally striped—in approximately that order (285, 297, 731a). These groups are by no means sharply defined but rather grade gradually into each other. In a summary of observations on over 700 X-ray-induced chlorophyll-deficient mu-

tants, Gustafsson (285) stated that about 50% were white; 18% were light- or yellow-green; 17% were virescent; and 13% were yellow. According to him (297), about one in 25 of the chlorophyll mutants is viable in the homozygous state. There were about 23 times as many induced chlorophyll variants as morphological, and about 20 times as many chlorophyll as physiological variants.

Cytological observations on spontaneous and X-ray-induced mutants have shown that there are differences in the plastids. According to Gustafsson (290), white mutants have small plastids, though the actual size varied from mutant to mutant. Plastids in virescent types varied from the base of the leaf to the tip, being less abnormal near the apex, but also varying among mutants. Yellow seedlings were intermediate in plastid development between the virescents and the whites, while the light- or yellow-green types sometimes approached the normal greens. In a "tiger" or zoned mutant the development of plastids depended on the intensity of expression of the zoning in individual plants.

Euler and co-workers (186, 187, 205) obtained results similar to those reported by Gustafsson, but, unlike the latter, found evidence of plastid degeneration. In one mutant the plastids were larger than those in normal plants, but, in general, there was a subnormality in plastid development which was correlated with the degree of departure from normal color. It was concluded (186) that chlorophyll deficiency resulted from the effect of genes on plastids rather than on chlorophyll itself.

Anyone who has worked with several chlorophyll-deficient types has observed fluctuations in the expression of the mutant characters. One of the chief environmental factors that affect the development of chlorophyll in defective types is temperature, and attention has been called to certain mutants that are especially affected by growing in different temperatures (139, 304). Light was also an important factor in chlorophyll development in a mutant described by Hallqvist (304). More intense light and higher temperatures increased the production of chlorophyll in this type.

The number of chlorophyll-defective mutants that have been studied is too large for each to be considered separately. However, almost without exception, spontaneous and induced mutations have been reported to be simple recessives. Some of the

exceptions will be considered individually. In a current study of bomb- and X-ray-induced mutants (731a), C. C. Moh (1950A) has found a considerable proportion of the mutants segregate in ratios significantly, and characteristically higher or lower than the theoretical 25%. A more complete treatment of the early literature on chlorophyll deficiencies, not only of barley but of other plants, has been given by Haan (302).

Chlorophyll chimeras are fairly common as a result of irradiation (cf. section on X-rays) and occasionally occur spontaneously (440, 456).

*Biochemical Studies*

Euler and co-workers made remarkable and almost unique contributions to the biochemical changes associated with induced and spontaneous mutants. Their observations were published in a series of papers dealing primarily either with pigments (186, 187, 191, 192, 198–201, 205, 496) or with enzymes (182, 184, 190, 193–197, 206–209, 211–215). Mackinney (506) extended the study to include pigments in chlorotic seedlings.

Chlorophyll content seemed to be closely correlated with appearance to the eye (201). In one yellowish mutant the average concentration was 1/3 of normal; but in yellowish mutants concentration of chlorophyll increased from base to tip of the leaves. In white seedlings no chlorophyll was detected with a spectrometer (191, 205). A greater difference was found in mutants between the ratio of chlorophyll *a* to chlorophyll *b* than was present in normal plants (496). There was evidence of definite ratios between chlorophyll contents of different types of mutants (496). Reduction in chlorophyll was associated with a reduction in tryptophane, but not necessarily with a reduction in gramine (93, 496) or arginine (188).

Although no chlorophyll could be detected in white seedlings with a spectrometer, another difference between white mutants was detected spectrometrically (199). An organic compound with an indol base was apparently responsible for this difference (200, 204, 205). The substance was present in greater concentration in mutant than in normal plants, and was thought to be a degradation product (205). This indol base was present in only two albino stocks.

The ratio of $O_2$ given off by normal and white seedlings varied from 2.2:4.0 on the fifth day of germination to 0.9:1.0 on the eighth day (214). Nilsson-Ehle (585) also observed that various parts of green plants used more oxygen than did corresponding organs of white plants.

The magnesium content was reported to be 30–40% less in white seedlings than in normal sibs (196, 212), but later studies (192, 207) on white, yellow and virescent mutants did not confirm the preliminary observations. Smith (724) found that albino maize seedlings were similar to barley seedlings that had been etiolated by being kept in the dark " in respect to their content of ether-soluble magnesium, phosphorus, and lipoidal material ". He felt that the albinism could not be attributed to a deficiency of these elements.

There was no apparent difference in iron content between leaves of normal and white seedlings of barley, but white leaves of *Tradescantia* contained twice as much iron as normal leaves (683).

The glucose content of green plants was 1.1–1.3 times that in yellow mutant seedlings (196, 197). This difference was not apparent in comparisons between normal and white or virescent seedlings. Chlorophyll-defective mutants contained considerably less porphyrin than normal seedlings (191), and a white mutant had only 1/5 as much hemochromogen as was present in normals (199, 207).

The biochemical studies by Euler and co-workers on enzymes were no less extensive. Catalase activity of extracted juice was found to be associated with leaf color, the activity in white seedlings being 1/2–1/5 that in etiolated normal-green seedlings (182, 184, 190, 195, 196, 206, 207, 209, 211, 212, 214, 585). The catalase activity varied among white mutants (214) and with age of the seedlings. The ratio of catalase in green to that in white seedlings increased during the first week of growth at 20–22° C. to a maximum of about 2.5:1 (195); then the ratio decreased for several days before again increasing (197). Seeds germinated in the presence of deuterium oxide had a reduced catalase activity (184). Light-green mutants did not show a clear reduction in catalase content (196). In other mutants, including some yellowish types, catalase activity was intermediate between that in normal and white seedlings (196, 206, 215). However, in one yellow

mutant the catalase activity was equal to that in the normal (207). In another mutant the activity was slightly greater than that in normal plants (196, 215). Normal cotyledons removed from the endosperm did not have a much greater catalase activity than mutant cotyledons (190). It has been reported (171) that there are marked differences between varieties as well as within varieties from year to year and season to season. Northern varieties had more catalase than southern varieties, and in crosses low catalase content was dominant.

There was no difference in the roots of normal and mutant white seedlings in their catalase activity, ability to reduce methylene blue, or bios content (202).

Comparisons between normal and mutant seedlings have also been made for certain other enzymes. Nilsson-Ehle (585) found little difference in the amylase content of homozygous or heterozygous normal and homozygous white seedlings. No clear difference was observed between normal and white seedlings with respect to peroxidase (196, 206) or redoxase (206). Dehydrogenase activity was greater in four-day-old than in week-old seedlings, but in most cases there was no difference between white and green seedlings of the same age (215). In one exceptional case, though, an X-ray-induced white mutant had twice the dehydrogenase activity usually found in normal-green plants. Dipeptidase activity in albinos was greater in both the scutellum and embryo than in normal seeds and seedlings (213). Albino and normal seedlings also differed in glutamic acid (203).

Sugawara (761) observed that the ascorbic acid content of albino seedlings was less than that in normal seedlings. Moreover, increasing the light intensity did not increase the vitamin C content in the white, but did in the normal seedlings. The ascorbic acid content of normal seedlings was correlated with brightness of the weather, with concentration of carbohydrates in the leaves and with concentration of $CO_2$ in the atmosphere (763). It was also greater under red and white than under blue and green light (762).

No distinct difference in starch content was found between white and normal sib seedlings (196). H. A. Borthwick and coworkers have unpublished results indicating that internodes of potentially green plants when grown in darkness attain only three-fourths of the length of albino plants.

Some effort was made to provide substances that would overcome the handicap of chlorophyll deficiency (193, 194, 207). Bios alone or with inositol had little effect, but inositol plus folliculin improved the growth of mutant seedlings. Zinc salts in addition to the inositol and folliculin had little effect. Adding 2% saccharose to Pfeffer's solution at first increased the catalase activity but did not prevent later decrease in catalase or color in a yellow mutant (207).

MORPHOLOGICAL VARIANTS—SPIKE CHARACTERS. Many of the genetic studies on barley have utilized naturally occurring morphological characters of the spike that distinguish the species and varieties of cultivated barley. A number of spontaneous and induced morphological mutants have also been used, although such mutants are relatively rare compared with the frequency of chlorophyll mutants (ratio 1 : 23, 297).

(14) Awns (1k—1,3; 1k2—1,3; 1k3— ; 1k4— ; k1—3; k12— ).

The genetics of awns and hoods has been a subject of considerable interest, for one reason, because awnless and hooded varieties do not usually (316) have the yielding capacity of awned types. However, the relationship of awns to yielding ability is still under study (37). Forms with each of the three types of spikes (awnless, hooded, awned) occur in nature and have also been found as mutants (453, 454, 612) or as segregates from crosses. According to Zhukovsky (911), most of the so-called "awnless" types are not truly awnless; they have short awns on the lower florets. He described a new completely awnless form but did not report any observations on the genetics of the character. Arlington Awnless is a variety that was obtained as a beardless segregate from a cross between two awned varieties (155). The hooded character ("trifurcate palea", "Kapuze") has also apparently occurred as a mutant under observation (314).

A review of the literature on the genetics of awns and hoods, together with studies on the geographical distribution of varieties with various types of awns or hoods has been made by Takahashi and Yamamoto (1949A).

In addition to the three types already mentioned there are naturally occurring forms with varying lengths of awns, and forms with widely differing degrees of development between awns on central and lateral florets. There are also types with three awns

on the same lemma; others have awns on the palea, or on outer glumes. Also length of awn seems somewhat correlated with height of plant and density of ear. All these things complicate the literature on genetics of awning. In general, however, it may be said that the awnless is dominant to the hooded, and both are dominant to the awned condition, though $F_1$'s are sometimes intermediate. Fraser (225), however, noted that slight awns were dominant over no awns (unlike awnless vs. awned or hooded). In some crosses between awned and awnless varieties the $F_1$ is hooded (846). As will be seen in the next few paragraphs, the genic basis of awns, etc. is simple in some crosses but not so simple in others.

Studies on the genetics of awns in crosses between awned and awnless types are numerous but not always in agreement. Austenson (42) found the $F_1$ of *deficiens* and Engleawnless to be almost awnless, and the $F_2$ easily classifiable on a 3 : 1 basis. Engledow (176, 177) had difficulty in classifying $F_2$ populations between a number of awned and one awnless variety (*H. inerme*), but $F_3$'s indicated that only one gene pair was involved—with heterozygotes intermediate. Similar results were obtained by Huber (372, 373). Engledow observed that time of sowing was important in the development of awns (177). Fung (240) also found that environment and modifying factors affected awn development, but felt that awns were largely dependent on a single gene pair in a cross between a fully-awned and an awnletted variety, Wong. Rimpau (659) noted hooded plants in the progeny of a cross between awned and awnless types.

Ubisch (842), Bussell (119) and Myler (564) concluded that two gene pairs were responsible for the difference between certain long- and short-awned (or awnless) varieties. Ubisch later (843, 845, 846) changed her ideas on awn inheritance, finally deciding that there were three genes for awns of varying length and a fourth gene for hoods. Miyake and Imai (453) concluded that there was only a single factor difference for length of awns in some crosses but that three genes determined the presence and length of awns in crosses between certain awned and awnless varieties. In crosses between an awnless six-rowed variety and a two-rowed awned variety, four gene pairs were used to account for the awn-classes observed. In a cross between six-row awned and awnless

varieties they explained the segregates on a three-factor basis. Ikeno (378, 379) also studied a six-row awned × awnless cross, and interpreted the results on a three-factor basis from a classification of 321 $F_2$ plants and an $F_3$ from each. It was felt that three pairs of genes were required to account for the various awn-length classes observed:

| | |
|---|---|
| ABC* | long-awned (lateral florets awnless) |
| ABc | fully awned |
| AbC | central florets short-awned (lateral florets awnless) |
| aBC | central florets short-awned (lateral florets awnless) |
| Abc | medium length awns on all florets |
| aBc | medium length awns on all florets |
| abC | awnless, all florets |
| abc | awnless, all florets |

In one cross So et al. (737) found evidence of four factors controlling the presence or absence of awns on the central florets. In seven other crosses the character seemed to be determined by three factor pairs. Another gene modified the expression of presence, absence and length of awns on the lateral florets.

Krajevoj (454) obtained an awnless type from a cross of a nearly awnless X-ray-induced mutant with an awnless Japanese variety. This awnless form, when recrossed to the awnless Japanese parent, produced an $F_1$ with short rough awns—and in $F_2$ segregated awnless and awned, both rough and smooth.

Leonard (482) reviewed some of the earlier studies on genetics of awns on lateral florets (262, 543) and presented some data of his own, all of which he thought could be interpreted as showing that appendages (awns or hoods) on lateral florets were determined by one gene pair. Leonard noted that normal was dominant over reduced appendages but that they were present only in six-row types. Dasananda (149) also believed that the presence, absence and length of lateral awns were determined by a single gene pair. This same gene pair was mainly responsible for the length of the awn on central florets, but evidence of (a) modifying gene(s) was found. Fung (240) seemed to feel that one factor was mainly responsible for the development of the lateral lemma appendages. Chia, on the other hand (127), interpreted his data on awn inheritance in crosses among varieties differing in awn

* Symbols are present writer's.

length on both central and lateral florets as the result of five gene pairs; one affected awn length on central florets, and four determined awnedness of lateral florets.

Awns vary not only in length but in strength. Takezaki (788, 789) studied these characteristics of awns extensively and observed their relation to length of ear. Four gene pairs were thought to govern the lengths of awn and ears. Long and short awns were stiff and brittle; medium and medium-long awns could be either stiff or flexible. Short awns were associated with short or medium ears; medium-long and long awns with long ears. Syakudo (1947A, 1948A) expanded the theory of Takezaki considerably. In addition to the three main gene pairs postulated by Takezaki (A, E, H), Syakudo suggested that there was a series of five alleles (i, $I_1$, $I_2$, $I_3$, $I_4$) which inhibited the development of awns. It was further postulated that three other gene pairs (M, $N_1$, $N_2$) modified the length or hardness of the awn. It was felt that this complex interpretation was necessary to account for the various situations in which awns on the central florets were many times longer than those on lateral florets, and where the reverse was true. Wang (872) also observed differences in awn strength. Long "strong" awn was dominant to short "weak" awn and was inherited monofactorially.

Takahashi (782) recently published a brief review of the literature on variations in awns.

(15) Elongated Glume (Awns on outer glumes or bracts) (e—1; e2— ).

This is a naturally occurring character (536) that several workers (42, 91, 149, 370, 868) agree seems to be conditioned by a single gene pair. Absence of the awns is completely dominant over their presence. Fung (240) noted that one main factor pair was probably responsible for awns on the glumes, but found transgressive segregates with awns longer than the long-awned parent.

(16) Dehiscent Awn (da—1; da2— ).

Dropping of awns at maturity was reported (373, 796) to be recessive and conditioned by one gene in some crosses and by two in others (799). Contrary to a rather widespread belief, there is evidence (9, 784) that the ash content of awns is not correlated with deciduousness.

(17) Hoods (" Kapuze " or " trifurcate palea ") (K—4).

Biffen (64, 68) crossed an awnless with a hooded variety and obtained an awnless $F_1$. In $F_2$ there were 27 awnless, seven hooded and seven awned plants (68). The appearance of awned types was " unexpected ", and it was suggested that one of the parents was possibly heterozygous. Rimpau (659) also reported awned segregates from a similar cross. Myler (564) later explained the appearance of awned segregates in the $F_2$ of such a cross on the basis of three gene pairs, two for awns and one for hoods. Tschermak (837) reported that $F_1$'s between hooded and awnless varieties were awnless, and in $F_2$, segregation was monogenic. Awnless forms were supposed to be AbC; hooded forms aBC; awned forms abC. Saunders and Moe (691) considered that some segregates from a cross of awnless and hooded types were potentially hooded because occasional abortive hoods developed on otherwise awnless plants.

Miyake and Imai (543) reported a segregation in $F_2$ of nine hooded: seven " normal " in a cross between a six-rowed awnless and a two-rowed hooded variety. Whether the " normals " were awned or awnless was not stated, but the segregation was explained on the basis of two complementary genes. Park (598) and Thatcher (811) crossed Arlington Awnless × Olds White Hull-less (a hooded variety) and found the $F_1$'s had reduced hoods; in the $F_2$ there was an almost continuous series of awn and hood development. A two-gene-theory was used to account for the types observed. One dominant factor (H) produced hoods; its recessive resulted in awns. A second factor in the dominant condition partially suppressed H, two doses of the dominant allele being more effective than one in suppressing H.

A great many workers have reported that the $F_1$ in crosses between hooded and awned forms is hooded, although in many cases more or less intermediate, and in $F_2$ there are three hooded : one awned plants (42, 63, 64, 68, 77, 78, 107, 115, 119, 146, 225, 233, 240, 242, 262, 308, 370, 373, 404, 408, 434, 493, 521, 522, 657, 660, 691, 733, 737, 801, 812, 843, 844, 868, 872, 874). Rimpau (659) noted the appearance of awnless plants in later generations of a cross between awned and hooded varieties.

Glinyany (262) found $F_2$ and $F_3$ segregations from a cross of hooded with an awned variety to be rather complex, but concluded that one gene was responsible for hoods. In the recessive

condition this gene promoted awns on all florets. A second gene, in the dominant condition, favored awns on central florets; and, as a recessive, on all florets. So et al. (737) found 9:7 ratios in some, and 3:1 ratios in other crosses between hooded and awned types.

According to Myler (564), two factors for awns must be present before the factor for hoods can develop the hooded condition. Ubisch likewise came to the conclusion that in some crosses hoods were dependent on one gene pair but that awns were determined by two (842, 843, 845) or three genes (844–846).

Carne and Limbourn (123) found what seemed to be a natural cross of awned × hooded. In the $F_2$ there were hooded and awned plants, and an intermediate class with hoods on short awns.

Savinskaja (692) also observed the $F_2$ of a natural cross (opined to be between plants of an Abyssinian, two-rowed, awned variety, *copticum,* and six-rowed, hooded Nepal), and noted that there were eight classes of individuals differing in hoods, awns, density of ear and color of seeds. Two classes differed from either parent, having hoods on central and short awns on lateral florets. These plants resembled var. *cornutum* Körn. Other classes had long awns on central, and short awns on lateral florets, but the reverse type was not obtained.

Michels (531) reported obtaining awned segregates in the $F_2$ of a cross between two hooded varieties. The ratio of hooded to awned plants was approximately 3:1. However, one of the putated parents had hulled, the other had hull-less seeds. The $F_2$ (?) was all hulled, contrary to the findings of a number of other workers who have studied hulled-naked hybrids. G. A. Wiebe [12] repeated the cross, using the same varieties, but was unable to confirm Michel's results.

There is considerable variation in the appearance of hooded plants (404), some varieties having hood-like structures on the awns, although the awns may be almost normal in length. These structures have been called "elevated" or "super-numerary hoods" by some workers; others have referred to barleys with the character as "curly", because of their appearance. Fung (240) from her own work and that of Biffen (63, 68), Lewis (490), and Ubisch (846), concluded that these awn-hoods were not readily analyzable genetically. It seems that possibly they are

[12] Unpublished observations.

dependent on at least two duplicate factors that are recessive to the factor for normal hoods and also recessive to the factor(s) for awns. The expression of the factors for super-numerary hoods was strongly affected by environment.

R. Takahashi (personal correspondence) has recently concluded that normal hoods (K), elevated hoods ($K^e$), and long awns (k) are governed by an allelic series of genes. Monohybrid segregations were obtained in the three possible hybrid combinations. A " subjacent " hood was recessive to long awn and determined by a gene which was independent of the K series. A cross of normal × subjacent hood gave 9 hooded : 3 awned : 4 subjacent hood in $F_2$.

(18) Brittle Rachis (Bt—2; Bt2— ; Bt3— ; Ws— ).

Two of the species of barley in the *cereale* section (*H. agriocrithon* and *H. spontaneum*) have fragile rachises. It has been known for a long time (493) that brittle was dominant over persistent rachis, and some have found the difference to be monofactorial (68, 225, 695, 800, Covas 1950aA). Ubisch (841, 843, 844) and Schiemann (698) opined that two genes for brittle rachis are present in *H. spontaneum,* although the data did not always fit a two-factor hypothesis very well (696). Schiemann (698) also found evidence of a third factor for brittle rachis in *H. vulgare,* but it had less effect than the two factors in *H. spontaneum.* Bussell (119) reported a ratio of 63 fragile : 1 non-fragile $F_2$ plant. Tschermak (834) found a ratio of 10.3 : 1, which he suggested might result from the segregation of three or four factors, but he thought (836) that in some cases two factors might account for the results.

Several (68, 74, 410, 493, 781, 841, 844) have obtained brittle-rachis $F_1$ plants from crosses between tough-rachis varieties. In $F_2$, 9:7 (410, 781, 841) and 7:9 (781) ratios were noted, further indicating that complementary genes were involved. Brittle $F_1$ plants backcrossed to the non-brittle parent varieties gave a ratio of 1 brittle : 1 tough (410). Takahashi (781, 1949A) studied 110 crosses among cultivated varieties and *H. spontaneum.* Crosses with *H. spontaneum* gave a fragile $F_1$ and a 3:1 ratio in $F_2$. Crosses of Oriental with European varieties gave mostly brittle $F_1$'s. Crosses of varieties from the same general geographical area were mostly non-brittle. In $F_2$, 9:7 and 7:9 ratios were observed in crosses among the cultivated types.

Johnson and Aberg (410) crossed two varieties of *H. vulgare* that were known to have complementary factors for brittle rachis with *H. agriocrithon,* and in both crosses obtained 3:1 segregations for brittle vs. tough rachis. They suggested that the two genes for brittle rachis in *H. vulgare, H. agriocrithon* and *H. spontaneum* may be allelic.

Ubisch (841) made a study of the morphology of brittle and non-brittle rachises.

Forms with a brittle rachis have also been reported in naked barleys (798, 800). Complementary factors for fragility were indicated in vars. *nudum* and *coeleste* (798), one of which was linked with B (Group 2) (798), but in some crosses the character was conditioned by one gene (800). This gene segregated independently of genes in Groups 1, 2 and 4. The gene was given the symbol Ws, although the writer is not aware of any evidence indicating that it is not one of the genes, Bt or Bt2, for fragility of spikes found in covered types.

Ziegenbein (912) concluded that two-row, smooth-awned, spring barleys were more prone to " shatter " than were four-row, winter varieties.

(19) Ear Width.

Biffen (65) reported that $F_1$ hybrids between narrow- and wide-eared varieties (from *H. vulgare* and *H. hexastichum* respectively) were intermediate, and in the $F_2$ the ratio was 1:2:1. According to Mather (517, p. 34 and pp. 97–101), there is a correlation between ear length and breadth, and internode length.

(20) Erectum Kernel Base (Er— ; Er2— ).

The presence of a transverse nick and bevelling at the base of kernels has been used to distinguish between certain botanical varieties. *Vernum* base, with a transverse nick, occurs in the dense ears of var. *erectum; falsum,* with a bevel, occurs in the lax ears of var. *nutans; spurium* base has neither nick nor bevel, and occurs also in *erectum* types. Descriptions and illustrations of the *erectum* and *nutans* bases as well as some of the variations were published by Bergal (61). Tschermak (837) observed that *vernum* was dominant over *falsum* base in $F_1$, but in $F_2$, intermediate types were present. The ratio of *vernum* and intermediates to *falsum* base was approximately 3:1. Schiemann (700)

also reported a single factor difference for *vernum* vs. *falsum* base, but with *falsum*-type dominant. Mall (511) studied several crosses that were interpreted as showing that *vernum* base was dominant in some, and *falsum* dominant in other instances.

Tedin (805) and Tedin and Tedin (807) found a mutant line in which an unexpected nick had developed. This nicking was monofactorially controlled. In crosses involving the mutant "nicked" stock with a nicked variety, an approximation to a 9:7 ratio for nicking was observed in $F_2$. It was suggested that the two genes might be weakly linked. One of the genes appeared to be associated with spike density.

(21) Glumes, Hairy (Gh— ; Pbg—3).

Hor (370) reported that one gene was responsible for restricting pubescence on the glume. Dasananda (149) concluded that there were probably three genes affecting the presence or absence of pubescence on this structure. Ratios varied widely in different $F_3$ populations. Waddoups (868) observed 1:1; 1:2:1; and 3:1 $F_2$ ratios for long vs. short glume hairs in different crosses. He concluded that as many as three genes might determine the character.

(22) Hairy Rachis (Hr—1; Hr2—5; Hr3— ).

Dasananda (149) concluded that pubescence of the rachis was determined by three gene pairs. These genes seemed to be associated with factors controlling pubescence on the glumes. One of the genes for hairy rachis was linked with a dominant factor for elongated glume (between 17 and 28% recombination) and with a factor for long internodes (34% recombination). Fung (240) reported complete linkage between a factor for rachis pubescence and the main gene for rough awns. She postulated a second factor for long vs. short rachilla hairs.

(23) Kernel Rows and Fertility of Lateral Florets (Allelic series $V^t$, $V^d$, V, v—1; $I^h$, I, i—4; $I_1$— ).

Harlan (311) classified cultivated barley into four species on the basis of fertility of the lateral florets:

*a*) Six-rowed barley, with all rows similar in fertility and development of hoods or awns (*H. vulgare*).

*b*) Intermediate barley, with partial fertility of lateral florets, though they never bear hoods or awns (*H. intermedium*).

*c*) Two-rowed barley, but with staminate lateral florets (*H. distichon*).

*d*) Two-rowed barley, with rudimentary lateral florets, devoid of sex organs (*H. deficiens*).

Harlan later (315) stated that if he were to make a new classification he would probably group them all into one species because the differences were determined by single gene pairs.

More or less similar classifications have been made before and since (399). All of the six possible combinations of crosses among the four types have been made and analyzed repeatedly (462, 518). The two-row phenotype is considered to be dominant over the six-row, although the heterozygotes are intermediate.

In addition to the types listed above, multiflorus forms have also been found (cf. Table 2).

Some of the earliest reports on hybrids in barley discussed the results of crossing two-row, six-row and *intermedium* types on the development and fertility of the lateral florets (64, 68, 75, 657, 658, 831, 835, 891).

The genetic basis of row number has been attributed by some to one factor pair with two-row types more or less dominant (42, 63–66, 68, 75, 82, 107, 115, 146, 175, 176, 225, 233, 242, 275, 308, 372, 404, 408, 434, 504, 511, 521, 522, 571, 638, 691, 693, 797, 806, 812, 858, 860, 872, 885). Others have considered fertility of lateral florets to be determined by two factors (48, 58, 119, 276, 317, 660, 808, 835, 842–846, 874). Six-row segregates have been obtained from crosses between two-row types (640), which suggests that more than one gene pair is involved. Still others have felt that the character was conditioned by three gene pairs (22, 250), or even four (127).

Matsuura (518) discussed fertility of lateral florets under the heading of "physiological characters", and Blaringhem (77, 78), as well as perhaps others, considered the character to be possibly non-mendelian. Many workers suggested that environment and modifying factors added to the difficulty of the classification. Hehn (345) found that fertility of the lateral florets was associated with or influenced by earliness.

Hor (370), Huber (373) and Woodward (898), among others,

have concluded that the number of rows of florets characterizing the several types of cultivated barley is determined by an allelic series of three genes (Linkage Group 1). Fertility of the lateral florets seems to be determined by another allelic series of three (898, 899) or four (373) genes (Group 4). The literature is somewhat confused because of the different species of varieties used in the crosses and because some authors distinguish two characters: two-row vs. six-rows, and fertility vs. infertility of the lateral florets; while others consider that there is only one character involved—i.e., fertility of the lateral florets.

The problem is certainly complicated by the fact that environmental conditions affect fertility, even of central florets, and (315, 319) also by the fact that two-row barleys occasionally have seeds in lateral florets. As an indication of the difficulty in arriving at a positive analysis, it might be observed that several workers changed their interpretations of the genetic basis of row number.

Veideman (858) attacked the problem of fertility of lateral florets with correlated genetic and microscopic studies. Histological observations led to the conclusion that sterility of lateral florets was associated with long thin pedicels. It was believed that fertility or sterility was a matter of nutrition, but the genetics of pedicel shape and hence nutrition was considered to be too complex for analysis.

Because of the many and conflicting publications on the genetics of kernel rows, it seems wise to refer the specially interested reader to papers by Leonard (483) for a more complete review of the literature, and by Woodward (898, 899) for his present solution of the problem. Earlier studies were summarized with much clarity by Matsuura (518).

So et al. (737) concluded that fertility of the basal, particularly the lateral, florets was controlled by two factor pairs in some cases and by three in others.

(23a) Large Lodicules (Glumellules).

Bergal (61, 1939A, 1947A, 1948A) and Bergal and Friedberg (1940A) made extensive studies on small, feathery structures lying between the lemma and the kernel. They are attached in pairs at the base of the floret and partially cover the germ. Apparently they have not been studied by many workers. These

"lodicules" vary in size, shape and degree of hairiness. The different types were thoroughly illustrated in several publications. They were considered to be useful in taxonomic classifications of species and botanical varieties. Of 405 $F_2$ plants from a cross between varieties differing in size of lodicules, 300 had large (*latisquamosae*), and 105 had small (*parviquamosae*) lodicules (1948A).

(24) Lax Spike (L—1,3,4; L2—3; L3—3,5; L4— ; L5— ; L6— ; La—3).

The degree of density in spikes varies widely in naturally occurring forms of barley. In addition a number of spontaneous and induced mutations have affected the compactness of ears. In some crosses lax ears are more or less dominant to dense ears and determined by a single gene pair. Biffen (64, 68) noted that hybrids between dense- and lax-eared types were about as lax as the lax parent. In $F_2$ there was a wide range of ear densities, with two modal frequencies centering around the parental types in some cases, but with transgressive segregation in some crosses. However, it was concluded that the data could be interpreted on a single-factor basis. Other workers have also studied crosses in which ear density was possibly determined by one gene pair (22, 77, 127, 149, 240, 339, 842, 868, 872). Wang (872) studied inheritance of density in ten crosses and concluded that, in at least nine of them, lax spike was dominant and governed by a single gene. Webster (878) found lax spike to be dominant in five crosses and possibly recessive in one.

Usually, it seems, ear density does not segregate sharply, and two or more gene pairs are postulated to account for the $F_2$ and $F_3$ populations observed. Ubisch (843, 844) opined that there was one main factor for ear density, plus two modifying factors. Still later she (845) and a number of other workers (168, 372, 498, 543, 864, 882, 884) decided that density was chiefly caused by two gene pairs. Hayes and Harlan (339) concluded that density was regulated by one gene in the cross Pyramidatum × Jet, two in Hanna × Reid's Triumph, and three in Hanna × Zeocriton—plus modifiers in each cross. According to Lunden (498), one of the two factors governing internode length shortened the basal internodes more than the more distal internodes, resulting in the

pyramidal spike shape of some varieties (see Lax Basal Internode).

Huber (373) decided that ear density was determined by four gene pairs, one of which shortened the distal internodes particularly. In his later studies Wexelsen (884, 885) thought that probably as many as six gene pairs regulated internode length. Other workers merely decided that the character was determined by multiple factors (370, 805, 807).

Some workers recorded transgressive segregation for ear density (78, 581, 885).

Krajevoj (456) reported a chimera in the $F_3$ of a cross between a dense- and a lax-eared type. Dense ear was recessive, and segregating generations gave Mendelian ratios.

Certain studies have dealt with variations in length of "lax-eared" types. Barbacki (48) stated that length of spike of long-eared forms was dependent on two cumulative factors in some crosses. David (150) observed that $F_1$ plants had spikes about the same length as the longer-eared parent, but the number of genetic factors determining the segregation in $F_2$ and $F_3$ could not be determined. Takezaki (788, 789) considered ear length to be determined by two factor pairs, both of which also affected awn length. Takahashi (1946A) also concluded that two genes which controlled spike density also affected spike, culm and coleoptile lengths.

(25) Lax Basal Rachis Internode (Lb—5).

In a cross between Cape and Wisconsin 38, length of the basal rachis internode was found to be governed primarily by a single factor pair with short internode being dominant. The factor was found to be linked with genes in Group 5 (345).

(26) Long Outer Glume (Log—1; log2— ).

Length of the glume was reported by Neatby (571, 572) to be governed by two gene pairs. One was a dominant, and the other a recessive that was inhibited by the gene for covered seeds.

(27) Naked (n—3).

Covered vs. naked is another of the few characters about which a large number of workers are in almost complete agreement as to

its mode of inheritance. The character is monofactorially determined with covered dominant over naked (22, 42, 64, 68, 107, 115, 119, 123, 146, 225, 233, 234, 242, 276, 308, 370, 373, 408, 420, 470, 521, 522, 524, 543, 571, 572, 660, 693, 758, 797, 806, 812, 831, 843, 844, 845, 868, 872, 874, 877). However, Harlan (315) felt that attributing the difference between covered and naked to a single gene an "over-simplification". A number of workers noted that heterozygotes were more or less intermediate (e.g., 68, 234, 493).

Differences in the ratio of kernel to hull are also apparently genetically determined (452).

Seeds of covered and six-row types remained viable longer than seeds of naked and two-rowed varieties (674, 675).

The available information and literature on adherence of the palea has recently been assembled by Takahashi and Yamamoto (1950bA).

(28) Branched ear (be— ; be2— ).

Tschermak (831) reported that normal was dominant over branched ear, but the gene basis was difficult to determine because of the instability of the branching. Bose (90) obtained branched-eared segregates from a cross between two normal-eared barleys. From $F_2$ and later generations data were obtained that fit a two-factor hypothesis. Branching was recessive and somewhat variable, so that not all the ears on a plant were affected; but branched ears bred true for the character within the limits of variation. The factors were apparently independent of genes for fertility of lateral florets. On the other hand, branching of ears was considered by Huber (373) to be probably controlled by one gene.

(29) Branched Spikelets.

Veideman (858) described and illustrated branching of the lateral spikelets which seemed to be genetic in some cases but not in others.

(30) Rough Awns (R—5; R2— ; R3— ; R4—3).

Smooth-awned barleys have been especially sought after, since awnless and hooded varieties do not yield so well as do awned types (316, 365) and because rough awns are disagreeable and dangerous. Awns thus appear to be important physiological or-

gans (343), but smooth-awned sorts seem not to be handicapped in this respect. There does, however, seem to be some association between barbs on awns and feathering on stigmas, so that smooth-awned varieties frequently exhibit a higher degree of sterility than rough-awned varieties (315, 900). Some of the naturally occurring smooth-awned botanical varieties were described by Regel (648, 649). According to Takahashi and Yamamoto (1949A), smooth-awned forms are not widely distributed, none being found in the Far East.

Mostovoj (550) studied the barbs on awns in some detail. It was found that barbs and their arrangement were varietal characteristics, although there was a good deal of natural variation. Barbs occurred singly or in groups, depending upon the variety and position on the awn. The differences in length of barbs between varieties varied from distinct protrusions down to " slow and minute " growths on " smooth-awned " barleys.

In a study devoted specifically to awn barbing, Friesen (235) concluded that there were four degrees of roughness: Rough, $AABBB_1B_1$; intermediate smooth, $aaBBB_1B_1$; smooth, $aabbB_1B_1$; and very smooth, $aabbb_1b_1$. Five crosses were studied, and segregation varied, depending upon the gene-makeup of the parents. A similar grouping into four types was made by Takahashi and Yamamoto (1949A), who briefly reviewed the literature on awn-barbing.

A number of workers have obtained $F_2$ data from crosses between rough- and smooth-awned varieties that satisfactorily fit a 3:1 ratio (42, 127, 146, 225, 240, 308, 312, 370, 479, 498, 521, 522, 531, 532, 639, 651, 733, 868, 872, 884, 885). In some cases the heterozygotes have been reported to be intermediate (135, 885). Hayes et al. (335, 342) concluded that there was one main dominant factor for rough awns, with modifying factors affecting the degree of roughness.

Others (127, 276, 413, 414, 672) have reported that rough awns were dependent on two factor pairs in some crosses, one epistatic to the other, giving a ratio of about 12:3:1 of rough- to intermediate-smooth- to smooth-awned $F_2$ plants. Sigfusson (716) obtained a 9:3:3:1 ratio, being able to distinguish two intermediate classes. Huber (373) reported that barbing was controlled by two gene pairs having additive effects. Crosses between Velvet and Trebi and Glabron and Trebi were reported to give 13 smooth- :

3 rough-awned $F_2$ plants (881, p. 343). David (150) thought that there was one main factor for smooth awns and another main factor inhibiting smooth awn. This interpretation was developed to account for segregations observed in $F_3$. The $F_1$ plants were rough-awned, and the $F_2$ plants were approximately 3 rough : 1 smooth. Hehn (345) found rough awns to be determined by one factor pair in some crosses, by two in others.

Vavilov (854) concluded that there were five or six pairs of genes that determined the number, shape and arrangement of barbs. Smooth-awned sorts had been found to occur in the Caucasus.

Colin, and Colin and Trouard-Riolle (135–137) reported that the $F_1$ between a smooth- and a rough-awned variety was rough-awned, but the degree of roughness varied among spikes on the same plants, some even being smooth. Segregation in later generations was not particularly clear-cut. It is difficult to evaluate their unusual observations.

Smooth-awned segregates were obtained by Bulavas (116) and Vavilov (854) from crosses between rough-awned varieties.

Johnson and Aberg (410) obtained evidence from crosses among two rough-awned varieties of *H. vulgare* and one rough-awned variety of *H. agriocrithon* that the genes for rough awns were the same in the two species.

Middleton et al. (532, 533) found an association between smooth-awnedness and spring growth-habit, though the association was not so close, but that winter-type smooth-awned strains could be obtained. Rough awns were conditioned by a single gene pair, but the writers did not give the factorial basis for spring growth-habit in their material.

Chia (127) drew attention to the row of barbs on the dorsal "midrib", which was determined by two gene pairs that were different from those affecting barbs on the edges of awns.

(31) Rachilla Length (Basal Bristle, Basalborste, Ventral Bristle) (Ra—5; Ra2— ; Ra3— ).

The basal bristle has been used as a taxonomically important character and has been studied in some detail by a number of workers (38–40, 57, 172, 780, 913, 914). It varies from 3/4 to 20 mm. in length (913) and is covered with pubescence that varies in both length and density. Bell and Carson (57) reported that

the length of the rachilla was controlled by about four factor pairs. Length of the rachilla was affected by environment and by density of the spike, and was also closely correlated with length of the rachilla hairs. Long rachillas usually had long bristle-like (Archer type) hairs; short rachillas usually had short woolly (Chevallier type) hairs. Ziegler (913) apparently spent considerable time in the study of variations in the basal bristle, many of which occurred on individual spikelets. These abnormalities were not inherited. Two distinct types were recognized, similar to those of Bell and Carson (above), and many intermediates were tested without any evidence of a heritable transition from one type to the other.

(32) Rachis Internode Number (rin—1; rin2—4).

The number of rachis internodes may be determined by one gene in some crosses (795), or at least two (233), or three (345), or one main gene and a modifier (773). Evidently one of the main genes for the character is in Group 1 (233, 773), and a second gene for the character is in Group 4, nearer a gene for mildew reaction than the factor for hoods (233).

(33) Short Rachilla Hairs (s—5).

Hairs on the rachilla are longest on those varieties with the smallest number (238). Long hairs are unicellular, short hairs are multicellular (39, 913).

Long-haired "bristly" rachilla is dominant over short-haired "woolly" or "glabrous" rachilla (172, 511), and a number of investigators have found the difference to be determined by a single gene pair (68, 74, 76, 115, 119, 146, 168, 175, 225, 240, 308, 370, 372, 408, 498, 521, 522, 660, 672, 693, 716, 733, 780, 842, 844, 845, 862, 864, 868, 882, 885).

Eikeland (168, cited by Wexelsen 885) thought that two linked genes were responsible for rachilla hairs, but, according to Wexelsen, other workers (864, 885), studying the same cross, concluded that only one gene pair was involved. McLennan (522) also felt that the character might be determined by complementary genes in some crosses.

Several workers (115, 149, 175, 370 and others) noted that the factor for rachilla hairs also affected pubescence on the glume. More recently Wiebe (Unpub.) found that in certain varieties from Chosen the relationship no longer holds. Hor (370) thought

that a second gene pair affected the distribution, or extent, of hairiness on the glumes.

Johnson and Aberg (410) obtained 3:1 and 1:1 ratios for rachilla hairs in $F_2$ and backcross populations of crosses between *H. vulgare* and *H. agriocrithon*. They concluded that the genes for long-haired rachillas in the two species were allelic.

Aufhammer (39) reported an abnormal variable type of rachilla pubescence that evidently was genetically determined. This paper and papers by Fruwirth (238), Isenbeck and Hoffman (399) and Ziegler (913) illustrate a number of types of variation in the pubescence on the " Basalborste " or in the rachilla hair itself.

(34) Teeth on Lemma Veins (G—1,3).

Several workers have found teeth on lemma veins to be dominant and conditioned by one gene pair (73, 74, 76, 77, 831, 885). Blaringhem (75, 76) found that the segregation of spines on lemma veins closely approached a 3:1 ratio in some crosses, but in other crosses various ratios were obtained, some of which did not seem to fit Mendelian ratios. Differences were observed between toothing on spikes on the same plant, and even between florets of a single spike.

Ubisch (842) distinguished three sizes of teeth, including one that could be seen only after magnification. She thought that there was one main gene for large teeth and that two alleles were responsible for less well developed types. In later studies toothing was attributed to two gene pairs (843, 844). Huber (372, 373) also decided on a two-factor explanation for the character. Part of the judgment was based on a 15:1 ratio in an $F_2$ that was further tested in $F_3$. Karpechenko and Ivanova (427) suggested that there was one main gene with other modifying factors affecting the classifications. The main factor was linked with the gene for wide glumes (Group 1), but the recombination percentage varied from 13.7 in $F_2$ to 41.5 in some $F_3$ populations. It was suggested that the range might have been affected by environmental conditions or modifiers.

Dasananda (149) distinguished between toothing on the first and second lateral veins of the lemma. A 3:1 ratio of plants with toothed : toothless second lateral veins was observed in the $F_2$ of some crosses, but in others three genes were required to account for all the ratios obtained.

(35) Unbranched Style (U— ; U2— ; U3— ).

Robertson et al. (670, 672) concluded that the difference between the smooth style of Lion and the feathery style of Coast was determined by three genes.

(36) Wide Glumes (w—1).

Evidently wide glumes are recessive to narrow glumes, and the difference is caused by one gene in some crosses (64, 68, 91, 225, 370, 401, 427). In other crosses the difference may be determined by two genes. Hor (370) obtained a 13 : 3 ratio of narrow : broad glumes in the $F_2$ of a cross between two narrow-glumed forms. Heterozygotes were intermediate. The data were interpreted to be the result of a dominant gene for wide glumes and another dominant inhibitor gene in the same stock. Modifying factors also seemed to be present. Schiemann (697, 699) likewise obtained broad-glumed segregates from crosses between narrow-glumed plants, and interpreted the observations on a two-factor basis. Rimpau (659) obtained a " macrolepis " form from a cross between a four- and a two-row type.

Records of two spontaneous mutations affecting the character have been found. Bose et al. (89) described a variety with awned broad glumes that was apparently obtained as a mutant. Miege (538) noted a spontaneous mutation to broad glumes on the central florets that left the glumes on laterals normal. Takahashi and Yamamoto (1949A) reviewed the literature on wide glumes and pointed out that the form is not widely distributed. No wide-glumed types were found in the Far East.

(37) Inner Glume Width.

Width and " ruggedness " of the inner glumes was considered by Huber (373) to be determined by two independent gene pairs.

MORPHOLOGICAL VARIANTS—PLANT CHARACTERS.

(38) Bloomless (Glaucous Ear, Glaucous Sheath, Waxless Head) (Ge— ; Gs— ; Wh— ; Wh2— ; W1— ).

Barley plants, as well as plants of other cereals, have a more or less distinct, whitish, waxy " bloom " on sheaths, leaves and spikes. Absence of this bloom has been found to be a monofactorial recessive. It may be that there are two genes for " bloomless "

which affect the stem and spike, or spike only (391, 401), and another gene that removes the bloom from the leaves and sheaths (297, 744, 828). Genes for "bloomless" have been found as a result of both spontaneous (401, 828) and radiation-induced (297, 744, Author [13]) mutation.

(39) Coleoptile Length.

Takahashi (777) studied the coleoptile length of 300 varieties collected from Japan and neighboring areas and found that they fell into two groups with respect to coleoptile length. One group had a mode around 25 mm. and the other around 43–46 mm. This difference was controlled mainly by a single factor pair with long coleoptile being dominant. Takahashi (1946A) and Takahashi et al. (1950A) observed that a semi-brachytic, "uzu" (uz), type was also distinguishable in the seedling stage by a short coleoptile with characteristic projections at the tip.

(40) Curved Peduncle (cr— ).

Erect peduncle is apparently dominant to curved (115, 503) and dependent on one gene (115).

(41) Dwarfs (br—7; D— ; m— ; uz—6).

Several types of dwarfs have been observed as spontaneous and induced mutants in barley. In most cases they have been found to be simple recessive characters (322, 543, 770, 783). However, Miyazawa (545) obtained a dominant dwarf mutant in a backcross of two normal plants. In later generations the ratio of sterile-dwarf : dwarf : normal was approximately 1 : 2 : 1. Dwarf plants were always heterozygous, and normal plants gave only normal offspring. The extreme sterile-dwarfs exhibited excessive tillering, slow growth, small stature, low resistance to cold and to *Erysiphe graminis*.

(42) Leaf Shape.

Miyazawa (546) found that width of leaf was intermediate in hybrids between narrow- and broad-leaved types. In $F_2$ the plants seemed to conform to a 1 : 2 : 1 ratio, but, according to the author, the results were not conclusive. The same author reported

[13] Unpublished observations.

observations indicating that long leaves were dominant over short leaves. From $F_2$ and $F_3$ data it was concluded that the character was determined by one gene pair.

(43) Liguleless (al—1).

A liguleless mutant was obtained by Lutkov (499) as a result of X-ray treatment. The auricle was almost normally developed, making it necessary to examine the plants carefully to detect mutants from normals. The character was a monofactorial recessive. Takahashi et al. (1950A) obtained a crossover value of 38% between a gene al for liguleless and v (Group 1). Tests with genes in Groups 2, 3, 4, 5 and 6 indicated absence of linkage.

(44) Right- and Left-handedness.

According to Compton (140, 141), an excess of barley seedlings have the first leaf twisted in the "left-handed direction". The twist of the first leaves did not appear to be influenced by the position of the seed on the ear, the twist of the first leaf of the parent plant, nor by the twist of the last leaf below the spike from which the seed was taken. In other words, right- and left-handedness did not seem to be hereditary. Ono (593), on the other hand, found an excess of right-handed grains (57.7% of the total). There was some correlation between handedness of the seeds and odd and even rows on two-row barley, but both odd and even rows of seeds gave an excess of right-handed grains.

(45) Hairy Leaf Sheath (Hs— ).

Pubescence on leaf sheaths was found to be conditioned by one gene pair with pubescence dominant (374, 786). The gene seemed to be linked with one of four genes for winter habit because winter types usually had pubescent sheaths. The amount of pubescence on the leaf sheaths has been reported to be affected by environment, although it is a varietal characteristic (40). Takahashi et al. (786) found that about 90% of the native Japanese covered barleys had hairy leaf sheaths. The naked varieties were almost all non-hairy, so it was felt that the naked and covered types could usually be distinguished in the seedling stage by means of the sheath hairs.

Takahashi has found that the factor for hairy sheath is closely

linked (6–7% recombination) with a factor for spring vs. winter habit. The linkage group has not been identified as yet (personal correspondence).

(45a) Fragile Stems (fs—5).

Takahashi et al. (1950A) reported a gene in Group 5 that resulted in stems that were easily breakable between the fingers.

PHYSIOLOGICAL VARIANTS. Genetic studies of physiological characters are considerably less numerous than studies of color and morphological types. However, such characters as earliness, winter-hardiness and yield, as well as a number of others, are of much interest, both to the agronomist and to the geneticist. Some of the characters with a more or less quantitative nature might be classified under other sections if their segregates were a little more clearly defined.

(46) Earliness (Ea—1; Ea2—5; ea3— ).

Time of maturity is a very important agronomic character because of its relation to seasonal changes in moisture, disease hazards, farm activity, crop rotations, yield, etc. Bakhteiev (44) tested 250 varieties of barley at 30 locations in the USSR and found that the length of the vegetative period ranged from 55 to 111 days. It was affected by location, day length and temperature. Rasumov (646) observed that early differentiation of floral structures was not particularly affected by length of day in early stages of growth. However, shooting and flowering were strongly hastened by long days. Borthwick et al. (1941A) observed that plants which were subjected to a 12-hour photoperiod were infertile, whereas plants in a 16-, 20- or 24-hour photoperiod were lighter in weight but produced seeds. Borthwick et al. (88) showed that a brief application of light of proper wave length and intensity during a long period of darkness produced an effect similar to that of long days in hastening flowering. Leopold and Thimann (485) found that low concentrations of auxin promoted early flowering and increased the number of flower primordia. However, the auxin could not overcome the effects of day-lengths that ordinarily prevented flowering. Higher concentrations inhibited growth and flowering. Coumarin, likewise, promoted

flowering in low concentrations but inhibited it at high concentrations (485).

Borodin (87) tested the effect of withholding N, P or K from barley in 18-, 12- and nine-hour days. Withholding N hastened flowering in long days, while a deficiency of P or K delayed earing. The C/N ratio varied from 5.4 to 16.5, but it was concluded that the C/N ratio alone did not account for photoperiodic response.

Increasing the sand content of the soil mixture hastened flowering (714).

One of the first genetic studies of early maturity (893) indicated that earliness was recessive, although the classification into early and late plants was not sharp. Mackie (503) reported earliness dominant in a cross between Chevalier (*H. distichon*) and Abyssinian (*H. deficiens*). In a cross between Svanhals and Lion, varieties that differed by 15 days in date of heading, Griffee (276) found earliness dominant and determined by a single factor pair. This factor was linked with the factor for number of rows (Group 1). Barbacki (49) and Neatby (572) also found evidence that a main factor for earliness was linked with the factor for two rows, but other factors affected the expression of the character (49). Two-rowed forms tended to be late, tall and dense-eared (571). Wexelsen (885) found evidence of linkage of one factor for earliness with row number (Group 1) and of linkage between another earliness factor and factors for rough awns and dense ears (Group 5).

In a study involving five crosses it was believed that earliness was determined by two pairs of genes in each cross (128). Earliness was dominant, but the degree of earliness depended on the number of dominant genes present. Others (345, 372, 413, 414, 571) concluded that earliness was dependent on two or more gene pairs in some crosses. Transgressive segregation for both lateness and earliness was noted.

Other studies suggest that earliness may be dependent on one gene (82, 801), two genes (150), three genes (572) or many genes (58, 318). Hehn (345) found earliness determined by one, two or three genes, depending on the varieties crossed.

Harlan and Martini (318), in a study of 351 $F_1$ hybrids in-

volving 27 parents, showed that whether earliness was dominant or not, and the degree of earliness or lateness, depended upon the particular varieties used as parents. Neatby (572) and David (150) obtained positive correlations between the mean dates of heading of parents and $F_3$ progenies.

Bell (56) stressed the relationship between physiology, heredity and environment in the expression of such characters as earliness. The discussion was based on a study of nine crosses, including species crosses, in $F_1$ and later generations. There was a tendency for earliness to be dominant in $F_1$, and there was a preponderance of early types in $F_2$. Some crosses "superficially suggested 3:1 ratios in the $F_2$", but certain segregations indicated a less simple interpretation. The expression of earliness was strongly affected by date of planting and other factors. Some crosses, particularly those involving *H. spontaneum*, showed pronounced transgressive segregation.

(47) Osmotic Value.

Buchinger (114) came to the conclusion that the osmotic value of sap from barley and wheat seedlings, as measured by sugar solutions, was determined more by the cytoplasm than by genes. This judgment was based on observed differences in reciprocal hybrids and in non-stability of pure lines. Zwoboda (915), on the other hand, concluded that the ability of seeds to germinate in a sugar solution was a heritable varietal characteristic.

(47a) Palatability.

Probably many workers have observed the distinct preference of rodents or other varmints for certain varieties in a nursery. So far as the writer is aware, no one has studied this problem, nor its genetic basis. Harlan (315) related an exceptionally clear-cut case of varietal preference in which two cows in separate experimental plots selected and ate the same varieties in each of two replications. He sagely emphasized the desirability of testing varietal preferences for both hay and grain.

Swenson (771) also observed distinct differences between varieties in the preferences of grasshoppers. Smooth-awned types, in general, seemed to be preferred over rough-awned varieties. There was also evidence that different species of grasshoppers had

different preferences. Barley was preferred over oats and wheat. Hermann and Eslick (353) reported that *H. bulbosum* was 95% destroyed by grasshoppers. In the same test, damage to 28 species of grasses ranged from almost 0 to 100%.

(48) Post-harvest Dormancy.

Length of the dormant period of seeds after harvest was stated by Larson et al. (473) to be a heritable character. However, no genetic data were presented. The rest period was longest in immature seeds and seeds stored at low temperatures. Freistedt (234) also studied post-harvest dormancy, testing 250 varieties of summer and winter types. Japanese varieties were especially likely to have strong dormancy. In some cases immature seeds grew more readily than fully-matured seeds. The character was considered to be recessive and controlled by one or two genes. Brown et al. (109), from a study of over 4,000 varieties, and others (153, 329, 909) concluded that post-harvest dormancy was a varietal characteristic, but did not study its inheritance. It was associated with winter growth-habit (315, 329, 909) and in some varieties (109) could be overcome only by removing the seed coat from over the embryo. The most extremely dormant varieties came from the Near East (109). Deming and Robertson (153) found dormancy in more six-row than two-row varieties. The character seemed to be associated with resistance to germination in the shock. Pope and Brown (636) prevented dormancy from setting in by inducing vivipary in immature seeds. Treating seeds with ultra-violet light (377) and low germination temperatures (551) hastened germination. The usual pretreatment before germinating freshly harvested seeds is to chill them for five days or so at 5 to 10° C. Some barley workers and seed analysts merely dry the seeds for ten hours or more at about 35° C. before starting them to germinate. Munn (551), however, found that better germination was obtained if the freshly harvested seeds were merely germinated at 15° rather than the usual 20° C.—omitting the chilling or drying pretreatment. This method has been recommended for official seed analysts (350). Ruge (682) reported that a solution of 2% $MnSO_4$ + 1% $MgSO_4$, combined with a low temperature for three to eight days, stimulated complete germination of freshly harvested seeds.

Germination may possibly be affected by various factors, including maturity and moisture content of the seed (234, 239, 551), and the maternal tissue, particularly the hull (303, 730).

(49) Waxy Starch (wx—7).

A character similar to the "waxy" that has been studied in maize, sorghum and rice has been found to occur as a monofactorial recessive in barley (308, 428). G. A. Wiebe, R. G. Shands and O. J. Webster have unpublished observations showing that wx is located close to $f_c$ in Linkage Group 7. Presumably the gene affects the form of carbohydrate that occurs in both endosperm and pollen, as is the case in maize, etc.

A photomicrograph of presumably normal barley starch and a number of other starches was published by Fall (216).

(50) Spring-habit of Growth (Sh—5; Sh2— ; Sh3— ).

Some investigators have found genetics of growth-habit to be rather simple, with spring-habit usually dominant. Others have found a number of complications, such as environmental influences, particularly light and temperature (180), correlations between growth-habit and cold resistance, incomplete dominance of spring-habit or even dominance of winter-habit, and modifying genetic factors.

Varieties of barley were classified by Takahashi (775, 776) as winter, spring, intermediate and pseudo-winter types. The last class included varieties that failed to ripen when spring-sown, but were unable to survive the winter. Hybrids between spring and winter types showed that spring-type was dominant and determined by a single factor difference. Schiemann (701) and Tschermak (837, 838) also reported monofactorial differences between spring- vs. winter-habit. A few varieties are capable of maturing satisfactorily in some regions whether sown in the spring or fall. Some "changeable" types that form a few spikes in late summer if planted in the spring were found to be associated with certain geographical regions (451).

Winter vs. spring growth-habit was found by Hoffman (359) to be determined by an allelic series with spring-type dominant. However, growth-habit was affected by factors for vernalization, photoperiodic response and vegetative habit that gave a rather

complex over-all picture of the genetics of winter and spring growth-habit. Borodin (86) found that varieties had characteristic responses to yarovization, but did not give data on the genetics of the differences.

Freistedt (234) found evidence that growth-habit was determined by one gene in some crosses and by two genes in others. Neither of these genes was linked with the gene for naked kernel. Huber (374), after studying crosses between spring and winter varieties for five generations, decided that winter varieties had one dominant gene and that spring varieties had three other dominant genes for culm production. Hehn (345) found growth habit to be determined by two factor pairs in some crosses and by three in others. Two of the factors were completely dominant for spring-habit, the third was incompletely dominant. Li (492) postulated a dominant factor S for winter type, an inhibitor factor I for spring type, and a series of dominant R factors for winterhardiness.

Ruppert (684) observed that spring growth-habit was dominant over winter-habit in barley (not wheat as given in the text of the paper [14]), but segregation in $F_2$ suggested that a number of factors were responsible for development of the character.

Of seven spring-winter crosses studied by Tokhtuyev (829), spring-habit was dominant in six, and winter-habit was dominant in one. In $F_2$ the six crosses gave a preponderance of spring-types, and the one gave a 3 : 1 ratio of winter to spring. Middleton and Chapman (532) found an association between growth-habit and the gene for rough awns, but did not determine the genic basis for growth habit.

A number of cases of winter-habit segregates from crosses between spring-type forms have been reported (242, 266, 267, 345, 435, 463, 465, 466, 856, 857). Gaines (242) observed this and accounted for the segregation by assuming that one of the varieties had dominant genes for winter-type but that their action was suppressed by inhibitor genes. Thus he interpreted the genetics of winter-habit on a two-factor basis. Vavilov and Kouznetsov (856, 857) and Kuckuck (463, 466) also obtained winter-type segregates from crosses between spring varieties. The $F_2$ segregation was not clear-cut, but in some $F_3$ families the segregation approached a monofactorial instead of a two-factor difference.

[14] Information provided by G. A. Wiebe.

Kuckuck (466) obtained 44 winter-type among 385 $F_2$ plants of spring by spring crosses, but the rosette habit of growth was not recessive and was dependent on more than one gene. It was concluded that there was a physiological (not genetic) association between habit of growth and winter-hardiness, i.e., delayed heading and winter-hardiness were associated. This conclusion is contradictory to results of some workers who found no association between growth-habit and winter-hardiness (see section on Winter-hardiness). There was transgressive segregation for both winter-hardiness and earliness (465). Kuckuck (466) also crossed the same spring varieties, H10 and H13, to a winter variety, H77. H77 × H13 gave a true winter type, while H77 × H10 was intermediate.

Neatby (571, 572) concluded that two spring varieties, Guy Mayle and Canadian Thorpe, had three different genes for winter-habit. All three had to be recessive for winter-habit to be expressed, and the genes were cumulative in their effects on earliness within the spring-habit phenotype. Kuckuck (463) gave a similar explanation for the appearance of winter-type segregates in a cross between true spring barleys. It was further postulated that each of the three genes for earliness was twice as potent in the homozygous as in the heterozygous condition.

In crosses involving spring types of 15 botanical varieties, Grebennikov (266, 267) obtained segregations for winter forms in four different combinations, although all $F_1$ plants were spring types. Different ratios of spring- and winter-type plants were obtained, suggesting that some varieties differed by two, three and four gene pairs for growth-habit. It was concluded that there might be as many as five or six genes for this character, all of which were independent of genes affecting winter-hardiness.

Khodkov (435) obtained winter- and semi-winter type segregates from crosses of two spring varieties, but attributed them to the fact that the $F_1$ plants had been grown under conditions that stimulated genotypic changes (per Lysenkoism).

Lutkov (501) obtained a winter-habit type of mutant by X-raying spikes of a spring variety. The mutant seemed to be controlled by a simple recessive gene. Didus (157) found a winter-habit form as a spontaneous mutant.

Li's (492) report on genetic studies on growth-habit was not available to the writer for perusal.

(51) Winter-hardiness and Cold Resistance.

As would be anticipated in the study of a quantitative character, the genetics of winter-hardiness has been the subject of conflicting reports. Schiemann (701) found the genetics of the character complex. Winter-hardiness was more or less dominant and independent of the gene for spring-habit. Types with dominant factors for both winter-hardiness and spring-habit could mature when sown in either fall or spring. Harlan (315), Bell (1944A), Li (492) and Grebennikov (267) also decided that there was no connection between genes for winter-habit and winter-hardiness. Kuckuck (463, 466), on the other hand, thought that there was a physiological but not genetic association between growth-habit and winter-hardiness. Tschermak (838) considered winter-hardiness to be predominant in $F_1$ and to approach a 1 : 2 : 1 ratio in $F_2$.

In a cross between a winter barley and a facultative spring or winter type, Andersson (20) obtained transgressive segregates that were more cold-resistant than either parent. The greater cold resistance was correlated with a higher sugar content in the leaves but not with a higher percentage of dry matter. Yasuda (907, 908) also found cold tolerance to be correlated with monosaccharose content. Potassium deficiency reduced the sugar content and the cold tolerance. Ziegenbein (912) reported transgressive segregation for winter hardiness in crosses between a winter variety, Kalkreuther, and spring barleys. On the other hand, several years' work failed to produce for Kuckuck (467, 469) any evidence of transgressive segregation for winter-hardiness in crosses between Middle-European barleys.

Several workers (234, 532, 533) found evidence of linkage between smooth awns and susceptibility to winter injury.

Christoff (134) showed that environmental factors (moisture content of the soil and fertilization of the soil) as well as varietal differences affected cold resistance under field and controlled conditions. Plants infected with diseases such as loose smut are more susceptible to winter-killing (315, 912).

Tavcar (793) observed that winter-hardiness was associated

with a low (deep) growing point. Varieties differed with respect to this character, but winter barleys as a group had a deeper growing point than did summer types. Cold resistance was also associated with a long vegetative period and with a somewhat greater dry matter content. Winter-hardiness was independent of the gene for naked seeds (797).

Distinct differences between varieties and hybrid selections in resistance to natural frost (326, 328, 415) and to artificial low temperatures (603, 614, 840) have also been observed. Peltier and Kiesselbach (603) found a considerable difference among seedlings from different varieties in their resistance to controlled low temperatures. The least tolerance seemed to occur about the stage when food reserves in the seeds were exhausted. Early varieties tended to be more susceptible to injury in the seedling stage than did late varieties (614). Greater tolerance for cold was acquired from continuous than from intermittent hardening temperatures. It is interesting to note that cold can cause a chlorosis (589), or cold and heat (850) and cold winds (653) can cause a chlorotic banding similar to mutant-type chlorophyll deficiencies.

Harlan (315) felt that the greatest resistance to cold temperatures at heading time was to be found in spring rather than in winter varieties.

QUANTITATIVE VARIANTS.

(52) Height of Plant (H—1,3).

Tall has been reported to be dominant to short stature and controlled by one gene (470, 543); partially dominant and determined by one gene (837); or by two gene pairs with cumulative effects (48). Ubisch (843, 844) obtained evidence that plant height was controlled by one to three genes, depending upon the parent varieties used in the crosses. Others (150, 413, 414, 571, 572) thought that height of plant was a hereditary character, but the factorial basis was not determined.

Plant height has been studied in connection with qualitative and other quantitative characters. Two-row segregates from the cross of two- × six-row types have been found to be taller than the six-row segregates (437, 638, 806). Tedin and Tedin (806) observed that two-row families from such a cross averaged ten cm. taller than six-row families. Plants heterozygous for the two-row,

six-row factor averaged taller than six-row, but shorter than two-row plants. The results were attributed to linkage between a gene for height and the two-row factor. Webster (877), on the other hand, found six-row segregates were taller than two-rowed. He also observed that plants with short-haired rachillas were taller than those with long hairs; plants with covered seeds were taller than those with naked seeds. In each case the difference was small but significant; hence it was concluded that at least three pairs of genes affected plant height.

(53) Kernel Weight (Size) (Kw—1,7).

As with other size characters, size of seed seems to be determined by a number of genes, at least two or three (48, 49, 480), as well as by environmental factors. Barbacki (49) found an indication of linkage between factors for type of ear and factors for 1,000-grain weight. Lejeune (480) obtained transgressive segregates in $F_3$ with larger as well as smaller seeds than the parent varieties. Large-seeded $F_3$ progenies tended to be more susceptible to stem rust than the small-seeded progenies. Kiessling (437) and Beaven (53) also considered grain size to be a varietal and heritable character. Nelson (574) noted a correlation between female parent varieties and bulked $F_2$ populations in the weight of 1000 kernels. Martini et al. (515) found that the rate of growth of seeds and final weight were varietal characteristics, but did not study the genetics of the differences.

Suneson and Riddle (767) and Woodward (900) found kernel size to be somewhat increased by partial sterility.

Biffen (68) and Fraser (225) found $F_1$'s of crosses between long- and short-grained plants had long grains. In $F_2$ there was a predominance of long-grained plants.

(54) Lodging Resistance (Straw Strength).

Straw strength is of interest because of its bearing on lodging. Dasananda (149) found a high correlation between the weight of straw per plant and breaking strength. These characters were controlled by several genetic factors, as well as being strongly influenced by environment. Weak straw was dominant. Bose et al. (91) found at least two genes were responsible for development and distribution of schlerenchyma, which was correlated with

lodging resistance. They also found weak straw to be dominant. On the other hand, Garber and Olson (247) reported no consistent correlation between development of schlerenchyma and lodging. Thickness of cell wall did seem to be correlated with lodging, but the number or area of vascular bundles, diameter of culms and thickness of culm walls were not. Tschermak (838) noted a correlation between spike density and culm strength, and transgressive segregation of both characters.

Brady (92) found no plant or straw characteristic of much value in indicating lodging resistance in oats. According to Brady, Berg (60) "found transgressive segregation in straw stiffness among the progeny of a cross between the fairly stiff-strawed Gold barley and an early, six-rowed, weak-strawed variety". Nilsson-Ehle (584) also saw evidence of transgressive segregation for greater straw strength.

Fertilization with nitrogen, phosphorus or potassium was found to affect cell-wall thickness and lodging (760). An optimum supply of N increased straw strength, but an excess decreased it. Increasing amounts of P and K contributed to greater straw strength, but heavy applications of P increased the susceptibility to mildew.

(55) Straw-grain Ratio.

Beaven (53) felt that the proportion of grain and straw was genetically determined, but did not postulate a genic basis for his belief.

(56) Tillering.

The number of culms per plant is a varietal characteristic, but it is greatly affected by environment (310, 484, 804). Barbacki (48) found profusion of tillering to be dependent on two cumulative genes. David (150), on the other hand, obtained evidence that tillering was controlled more by environmental than by genetic factors. The number of culms per plant was affected by earliness, spacing and by the two-row, six-row gene pair. Tedin (804) also concluded that two-row varieties clearly had more tillers than did six-row sorts. Kiessling (437) found little evidence of association between the two-row, six-row factor and tillering. Powers (638) noted some evidence of interaction between factors for number of spikes and factors for color of glumes, num-

ber of kernel rows and growth habit, but concluded that the interaction was so variable that use of the qualitative characters as a means of selecting for number of spikes or any of three other quantitative characters would be of doubtful value. Tedin (804) reported that large seeds produced plants with more tillers than did small seeds. However, plants with a large number of tillers tended to produce smaller seeds. Plants with a large number of tillers produced spikes that were more dense.

Beaven (53, p. 325) was of the opinion that tillering capacity was an inherited characteristic, but did not report its genic basis. He was also of the opinion (p. 332) that "Viability—ratio of number of surviving plants on unit area to number of seeds sown" was a genetically controlled character.

Hubbard and Harper (371) reported that clipping (to simulate grazing) reduced the number of tillers. Leopold (484) found that conditions, such as short days, favorable for the development of auxin, or injection of auxin, reduced tillering whereas destruction of the apex, irradiation, coumarin and tri-iodobenzoic acid (which "oppose the action of auxin") resulted in increased tillering. Phosphate deficiency reduced tillering (95).

For a general study of a number of environmental factors that affect tillering in wheat and several other grasses, and for a considerable list of references on the subject, the reader is referred to Gardner (248).

(57) Yield.

Yield is one of the most important agronomic characters, so it is little wonder that there should be considerable interest in its genetic basis. Beaven (53, p. 116) stated that "there may be differences in value between two races in any one year, due to the inherited characters of the seed, amounting to at least 20 per cent". Bachteiev (45) made a number of hybrids among nine varieties and found that $F_1$ plants ranged in yield from 36% above to 53% below the yields of the parent varieties. In $F_2$ the values were 15% and 36%; and in $F_3$, 14% and 17%, respectively.

Immer (387) found that an average increase of 27% in yield per plant in six crosses between varieties diminished to 24% in $F_2$, 13% in $F_3$, and 5% in $F_4$. The yield of the highest-yielding $F_1$ was more than twice that of the lowest-yielding, and the pos-

sibility of using yields of replicated $F_2$'s as a basis for selecting high-yielding crosses was suggested. However, the yields of individual $F_2$ plants was considered to be unreliable in indicating yields of $F_3$ progenies (388). From a study involving $F_2$ populations from crosses of four varieties on each of 20 varieties, Nelson (574) concluded that there was a "heritable fraction" which contributed to the differences in yield. The yields ranged from 31% below to 73% (average 16%) above the mean yields of the parents.

Umeya (847) reported distinct heterosis in crosses between plants of the same variety, and attributed at least part of the hybrid vigor to the fact that the parent plants were grown under different conditions. Mather (517, pp. 33–37) presented data of U. Philip on intervarietal crosses in which it was evident that there was heterosis (as measured by ear length and breadth, and internode length) in $F_1$, and segregation in $F_2$ and $F_3$.

David (150) found no "good" evidence of segregation of genes for yield in any of five crosses. On the other hand, Wiggans (892) thought that there were strains even within some varieties that differed significantly in yield. There was also considerable difference in variability in varieties. Others (360) likewise have found evidence of genic control of yield, which may take the form of a number of cumulative factors (48, 49). It has been reported (270, 271) that there are differences between varieties in their ability to utilize applied fertilizers. A hybrid variety seemed "to inherit specific manurial efficiency from both parents" (271).

In studies involving a sister crop, wheat, Engledow and Wadham (178) cited such achievements as combining quality and high yield in one variety through hybridization of two varieties that possess only one of these characteristics as proof that yield is a heritable character.

According to Raum (647), dense types outyield lax varieties under favorable conditions, but the reverse is true under unfavorable conditions. There was also evidence that many-rowed varieties had a genic basis for higher yield than two-row types, but the difference found expression only in favorable years. The average yield per ear of ten six-row varieties was almost 50% greater than for 21 two-row varieties. Powers (638) likewise observed

evidence of interaction between the factors for yield and factors for certain qualitative characters. However, the interaction was variable and of questionable value in practice. Leasure et al. (477) found some correlation between yield and: *a*) height of plant, *b*) length of ear, and *c*) test weight, but considered the correlations to be too weak to be of much value in selecting for yield.

Suneson (1949A) and Suneson and Wiebe (769) found a lack of correlation between yielding ability in pure stands and the ability to compete in mixtures. Furthermore the variety Atlas, which comprised 88% of the population after growing 16 years in the mixture, "had the poorest leaf disease record" of the four varieties composing the mixture (Suneson, 1949A). The results were emphasized as limitations of the bulked population method of breeding.

GENETICS OF DISEASE REACTION. Disease resistance is one of the most valuable characters of economic plants, and was part of one of the first genetic studies with barley (67). Since these early experiments of Biffen, outstanding work on genetics of disease reaction has been done on this crop plant. It was also suggested by Vavilov (852, 853) that disease reaction could be used as a genetic test.

The works of Ausemus (41) and Dickson (156) are excellent sources of information on and citations to literature on the genetics of diseases in barley. A thorough but brief review of literature on the genetics of disease reaction, not only of barley but also of a large number of other species, was prepared by Hansen (307). More complete treatments of the subjects of disease organisms, host-parasite relations and methods of study as well as genetics were prepared by Roemer et al. (678) and Gäumann (1946A). A large portion of the treatise of Roemer et al. (678) was composed from the standpoint of identifying the organisms causing the diseases. However, each organism was favored with a brief discussion dealing with genetics of and breeding for resistance. Host plants, including barley, were more or less incidental in this approach.

In most cases Dickson (156) has been followed in the matter of nomenclature of pathogens.

(58) Bacterial Blight (*Xanthomonas translucens* (L. R. Jones, A. G. Johnson, and C. S. Reddy) Dowson).

The writer found very little on the genetics of the reaction to this disease. Hehn (345) reported that susceptibility seemed to be associated with earliness.

(59) Net Blotch (*Pyrenophora teres* (Died.) Drechs).

Heschele (354) studied the reaction of a large number of varieties to the net blotch pathogen and concluded that immunity was a Mendelian varietal character.

(60) Rusty Blotch (*Helminthosoporium californicum* Mackie and Paxton).

Resistance to this disease was reported to be conditioned by a single dominant gene (503, 504).

(61) Spot Blotch (Foot and Root Rot, *Helminthosporium sativum* Pam., King, and Bakke) (H1—1; H12—2; H13—5).

*H. sativum,* of which there are at least four physiologic forms, causes leaf spots, rootrots, seedling or "late blight", and discolored seeds of barley and a number of other grasses (130). The pathogen is widely distributed geographically, and a number of host and environmental factors affect its pathogenicity (Dosdall 1923A). There are also a number of other pathogens which produce root- and footrots (Sprague 1948A). Histological as well as other symptoms of the disease were reported in some detail by Mead (523). Arny (36), from seedling tests in $F_2$ and $F_3$ populations from several crosses, decided that reaction to the pathogen was controlled by one factor pair, with susceptibility dominant. There was no apparent linkage between this gene and genes for black chaff, rough awns, long rachilla hairs or stem rust reaction. There was some suggestion of linkage with genes for a xantha mutant and with reaction to stripe diseases. On the other hand, earlier reports indicated that in some crosses resistance was dominant and conditioned by more than one gene (276, 335, 336, 337, 341, 342). Griffee (276) noted transgressive segregation for both susceptibility and resistance. He thought that one variety, Svanhals, had at least three genes for resistance—one linked with

the six-row factor (Group 1) one linked with a factor for rough awns (Group 5) and one with a factor for white glumes (Group 2).

Waterhouse (874) noted that varieties which were resistant to leaf rust were also resistant to spot blotch.

Several spontaneous mutants with increased resistance to *Helminthosporium* were reported by Didus (158). This would suggest that resistance was recessive in these cases.

Porter (637) found that the effect of the pathogen on seed germination could be partially controlled by treating the seeds with 1% ethyl mercury phosphate. Eaton (165) reported that the disease did not develop when boron was omitted from the culture solution.

(62) Ergot (*Claviceps purpurea* (Fr.) Tul.).

Infection with ergot is favored by cool moist weather which prolongs flowering (833), and by sterility (853; Author, unpub.). Varieties differ in genetically determined morphological and physiological characters that affect susceptibility to ergot, e.g. naked are more susceptible than covered varieties (833), but there is no evidence of varietal resistance to infection (156, p. 158).

(63) (Powdery) Mildew (*Erysiphe graminis hordei* El. Marchal) ($M1_a$—2; $M1_b$—2; $M1_c$—2; $m1_d$—2; $M1_g$—4; $M1_h$ — ; $M1_k$—2; $M1_m$—2; $ml_n$— ; $M1_p$—2; $ml_w$— ; $M1_y$ — ).

Extensive studies on genetics of mildew reaction have been carried on by Briggs et al. at the California Agricultural Experiment Station, Davis. These investigations have resulted in outstanding achievements in the study of disease reaction. Twelve genetic factors (nine dominant or incompletely dominant and three recessive) for reaction to race 3 of the pathogen have been identified (96–101, 220–222, 748). One recessive factor, $m1_d$, was linked with one of the dominants, $M1_p$, and both were linked with a factor, $a_t$, for albino seedlings in Linkage Group 2 (98). Two dominant factors, $M1_a$ and $M1_k$, were linked with about 10% crossing over (100). $M1_a$ was inherited independently of a gene for short-haired rachilla (Group 5). $M1_g$ was linked with the

factor for hoods and a factor for blue aleurone in Group 4 (101). Freisleben and Metzger (233) probably studied the same gene as $M1_g$, calling it $Er_{cp}$, for reaction to mildew races 1 and 4, finding 16% recombination with K (Group 4). There was also evidence of linkage of both K and $Er_{cp}$ with one of at least two genes for rachis internode number.

Honecker has also conducted extensive studies on genetics of mildew reaction (363, 364, 366–368). Early observations indicated that resistance was a monofactorial recessive (363), but later tests with a larger number of host varieties and more races of the pathogen suggested a different and more complex interpretation. Environmental factors, particularly light and temperature, were shown to be important in the expression of resistance (364). With weak light and low temperature, resistance was recessive; with strong light and higher temperatures, resistance was dominant.

In a paper published in 1938 (366), seven degrees of susceptibility to mildew were distinguished. Resistance or immunity was dominant or recessive and determined by one, two or more genes, depending upon the varieties and races studied. Immunity tended to be monofactorial and resistance polyfactorial. Reaction to the pathogen was affected by genes for necrosis, necrotic flecking and chlorosis, as well as by at least three modifying factors (364, 367). Breeding for resistance to mildew was complicated by linkage (368).

Still more extensive tests with nine races of mildew revealed further complications in the interpretation of the genetics of mildew reaction (367). Variety Pflugs Intensive had resistance to race A that was controlled by a single semi-dominant factor, but was susceptible to race B. Ragusa b was resistant to both races A and B. Resistance to both races was possibly determined by a single dominant gene, but this gene was not the same one that conditioned resistance of Pflugs Intensive to race A. Variety CP10321 had a partially recessive gene for resistance to race D, the gene being the same one that was semi-dominant in Pflugs Intensive for resistance to race A. Development of mildew on the plants was affected by chlorophyll deficiencies and by at least three modifying factors.

A number of other workers have also reported observations on

the genetics of mildew reaction. Straib (756) found resistance to mildew to be determined by a single gene pair. Crosses between resistant Goldfoil and four varieties that were susceptible to race 4 gave ratios of 3 susceptible : 1 resistant plant in $F_2$ (159, 160). The observations were confirmed by $F_3$ tests. Jensen (407) came to a similar conclusion after a study of two other crosses involving Goldfoil as the resistant parent. Resistance to races 6 and 7 was controlled by a single incompletely dominant gene (818–820). This gene is apparently different from the seven reported by Briggs et al. because one of the resistant varieties, Nepal, is susceptible to race 3. No evidence of linkage was found between the factor for resistance and the factor for naked seeds (Group 3), hoods (Group 4), long-haired rachilla (Group 5) or six-rows (Group 1). Five wild species (*H. gussoneanum, H. jubatum, H. murinum, H. nodosum, H. pussilum*) were immune to race 6 (818).

Two independently inherited factor pairs seemed to control the reaction to mildew (predominantly race 6) in a cross involving susceptible Manchuria and resistant Chevron (345). The genes appeared to be additive in increasing resistance.

Vallega and Favret (849) and Favret (220) found in crosses with Trebi that the immunity of Monte Cristo to Argentine race 1 was conditioned by one main dominant gene. On the other hand, the resistance of Nigrate was the result of an incompletely recessive gene and at least one recessive modifying factor that intensified the resistance. Crosses between several resistant varieties gave only resistant plants in $F_2$ (Favret 1949A).

Favret (222) recently summarized the information available on 12 factors for mildew reaction to three physiologic races: Calif. 3, and Arg. 1 and 2. Most of the genes have similar reactions to Arg. 1 and 2, but these reactions were different from the reaction to Calif. 3. For example, most of the genes that gave resistance to Calif. 3 permitted susceptibility to Arg. 1 and 2. $M1_m$ gave resistance to all three.

Biffen (67) found that in the species cross, *H. spontaneum* × *H. hexasticofurcatum,* the susceptibility of the male parent to mildew was dominant. Data from an $F_2$ progeny of 79 plants suggested that a single factor was involved. Results obtained by Hoffman and Kuckuck (360) in some crosses with *H. spontaneum*

suggested that the immunity of this species was determined by a single dominant gene, but in other crosses the $F_2$ data did not fit a 3:1 ratio, so modifying genes were postulated. In one cross with a resistant Japanese barley, transgressive segregation was obtained.

Nishikado et al. (1949A) studied the mildew reaction of 807 varieties collected from various parts of the world. Resistant types came mainly from Europe and America. Hull-less varieties were not resistant, but presumably resistance could be introduced by crossing with hulled sorts. Mains and Dietz (509) studied the reaction of 40 varieties to five physiologic races of the pathogen, but did not determine the genetics of the differences. Three varieties were very resistant, 13 others more or less resistant, to all five races. The mildew reaction of over 200 varieties in six (in some cases seven) years was reported by Poehlman (619). The genetics of differences was not studied in this case either. Sarasola et al. (1946A) found 14 varieties or hybrids among about 270 that were tested which gave a resistant or immune reaction to Argentine race 1.

Suneson (1949A), by comparing the yields of Atlas and mildew-resistant Atlas 46, considered that mildew probably reduced the yield of susceptible Atlas about 15%.

Mackie (502) concluded that susceptibility was not affected by considerable changes in environmental conditions. Nor were there any clear morphological differences between leaves of varieties differing in susceptibility. Contrariwise Tapke (1949A) felt that susceptibility to infection was associated with tenderness of the tissue—which was not entirely determined by age but partly by the environment. Eaton (165) reported that mildew was absent from plants supplied with boron in the culture solution.

Hammarlund (1925A) found that wheat mildew (*Erysiphe graminis tritici* Marchal) could infect barley leaves through wounds, but not uninjured leaves.

(64) Leaf Rust (Dwarf Rust) (*Puccinia hordei* Otth.; *P. anomala* Rostr.; *P. simplex* Korn. Eriks.) (pa—1; pa2— ).

Mains and Martini (510) determined the reaction of an extensive number of varieties of barley to *P. anomala*, but did not study the mode of inheritance. Their observations and those of

Hey (355) should serve as a valuable basis for such studies. It has been reported (507) that the pathogen infects only varieties of cultivated barley and *H. spontaneum.* Other wild species and species of related genera were little if at all infected. Hassebrauk (332), however, found that the pathogen infected *H. murinum* and *Avena strigosa.* Eight physiologic forms of *P. simplex* were reported by Hey (355). Some barleys were resistant at low, others at high, and still others at all temperatures. Certain varieties segregated for resistance, but the genic basis for the segregation was not established. Straib (1936A) reported that the degree of infection with *P. hordei* varied with the temperature, variety and biotype. In general, susceptibility increased as the temperature increased from 12 to 21.5° C. Peterson et al. (607) recently published scales that would be helpful in distinguishing phenotypic classes of leaf and stem rust-affected plants.

Henderson (1945A) tested 246 varieties that appeared to be resistant in a field planting by artificially inoculating them with *P. anomala,* and found that 125 of them had only a trace to 5% of leaf rust. Most of the resistant varieties were from North Africa and were susceptible to spot blotch (*Helminthosporium sativum*), but seven varieties were resistant to both diseases. Eight of nine varieties seemed to have the same incompletely dominant gene, Pa, for resistance, while the ninth gave a ratio of 15 resistant : 1 susceptible in some crosses, indicating the presence of a second factor, Pa2, for resistance. Pa was not linked with N (Group 3); K, B1 (Group 4); R, S (Group 5), and Pa2 was not linked with B1 (Group 4) or R (Group 5).

Plants from all "3 main species" of barley (*H. hexastichum, H. tetrastichum, H. distichum*) were reported by Straib (756) to be resistant to dwarf rust, *P. simplex,* although no highly resistant winter barley was among those tested. Resistance was conditioned by a single gene pair, but in some cases the resistance varied from greenhouse to field tests. Honecker (368) concluded that there was probably a partial linkage between factors for number of rows and factors for resistance to dwarf rust. Waterhouse (874, 1948A) tested over 110 varieties of the four species of cultivated barley and found resistance to *P. anomala* completely dominant and dependent on a single factor pair. This factor did not seem to be associated with the factor for hoods or covered seeds.

Of the 26 strongly or moderately resistant varieties, all but one belonged to *H. vulgare*—the one was a variety of *H. distichon*. *H. spontaneum* was completely susceptible and *H. murinum* highly resistant. Varieties that were resistant to leaf rust also tended to be resistant to spot blotch, a result contrary to the findings of Henderson (1945A). Mains and Martini (510), on the other hand, found no correlation between resistance to leaf rust and resistance to mildew.

Others (876) reported that in some cases resistance to *P. anomala* was determined by two factor pairs.

(65) (Orange) Leaf Rust (*Puccinia triticina* Eriks. *rubigo-vera* (DC.) Wint.).

Resistance to *Puccinia triticina* was found to be completely dominant and dependent on a single factor (874). In these observations there appeared to be a correlation between resistance to leaf rust and resistance to spot blotch. In another report (392) resistance to leaf rust was determined by a single Mendelian factor, but the stability of resistance varied with varieties. Some varieties also changed in reaction during development of the plants.

There may be a relationship between chromosome number and resistance to leaf rust. Barley species with 14 and 28 chromosomes were more susceptible than one species with 42 (412). Other workers (332, 508, 875, Vallega 1947A) have likewise observed distinct differences in the reactions of wild and cultivated species to the pathogen. Cultivated varieties were not wholly susceptible, but varied in the degree of infection (412). For an exhaustive treatise on the taxonomy and host specialization of the pathogen, the reader is referred to Mains (508).

(66) (Black) Stem Rust (*Puccinia graminis* Pers.) (t—7).

Resistance to stem rust is apparently inherited as a simple dominant in some crosses (107, 345, 480, 639, 651, 711, 712, 733, 878). One variety, Peatland, had a single gene that determined both seedling and mature-plant resistance to races 19, 39 and 56 (107). This gene was located in Group 7.

In 37 $F_1$ hybrids between resistant and susceptible varieties, Waterhouse (1948A) noted that resistance to race 43 was dominant. Contrariwise susceptibility to races 34 and 45 was domi-

nant. Later generation tests were not made. There was no correlation between resistance to stem rust and resistance to leaf rust or mildew.

According to some writers, seedling reaction can be used to indicate mature-plant reaction to the pathogen (107, 390). Reid (651), however, using one of the same varieties (Peatland) studied by Brookins (107), concluded that mature-plant reaction to a mixture of races was monofactorially determined with resistance dominant; but seedling reaction to race 56, also studied by Brookins, was monofactorially controlled with susceptibility dominant. Consequently seedling tests with race 56 were considered valueless as aids in selecting lines for field resistance. Newton and Brown (576) concluded that mature-plant resistance was associated with age or maturity of the particular tissue. That is, young rapidly-growing regions of older plants exhibited the seedling type of reaction.

Tschermak (837) reported that susceptibility tended to dominate over immunity to stem rust.

Recently reported observations of Lejeune (481) indicated that resistance to a new, virulent race, 15B, was governed by the same gene or genes that control reaction to other races of stem rust.

Varieties of barley were reported to vary considerably in their reaction to stem rust of rye, but the genetics of the reaction was not reported (143). The pathogen was found to occur on two wild species, *H. jubatum* and *H. pusillum.* Vallega (1947A) observed reactions ranging from high resistance to complete susceptibility to *P. graminis tritici* in tests with seven wild species.

(67) Stripe Rust or Yellow Rust (*Puccinia glumarum* (Schm.) Eriks. and Henn.).

According to Tschermak (837), susceptibility to yellow rust was more or less dominant. Murty (562) found resistance dominant and governed by two gene pairs. There was no correlation between rust reaction and size or number of stomates or number of epidermal cells. Straib (758), in a study of the $F_1$ and $F_3$ generations of 11 crosses in their response to four races of *P. glumarum hordei* and *tritici,* found that resistance to one or more races was dominant in some crosses and conditioned by one gene pair. In other crosses at least two gene pairs seemed to deter-

mine the reaction, and resistance was not always dominant. Plants resistant to dwarf rust were also resistant to yellow rust (756).

Bever (62) determined the reactions of 365 varieties to the pathogen in field and greenhouse tests, but did not study the genetics of the differences. Infection decreased with decreasing light intensity and with increasing day-length (1934A). Poehlman (619) also observed the field reactions of about 250 varieties to the disease in two different years, but did not study the genetics of differences. Straib (1935A) tested 185 varieties for seedling reaction to 13 races. Only a few were resistant or immune to two races, 23 and 24. However most of the varieties were resistant or immune to the other races. One variety was immune to 25 races. Vallega (1947A) found that most of the seven wild species tested were more or less susceptible to *P. glumarum.*

(68) Scab (Fusarial Blight) (*Gibberella saubinetti* (Mont.) Sacc. or *Gibberella zeae* (Schw.) Petch, *Fusarium* sp., and *Helminthosporium sativum* Pam., King, and Bakke) (sc— ).

No information was found on the genetics of reaction to scab, except that there are resistant varieties (132, 389). Christensen et al. (132) found no correlation between resistance to scab and resistance to spot blotch. Porter (637) showed that the reduction in germination caused by infection with *G. saubinetti* could be largely controlled by treating the seeds with ethyl mercury phosphate.

(69) Scald (*Rhynchosporium secalis* (Oud.) J. J. Davis).

Riddle and Suneson (655) reported a wide range among varieties as to their susceptibility or resistance to the disease, and a case where resistance was transferred to a susceptible variety by backcrossing. They did not, however, report on the genic basis for the reaction. Suneson (1949A) considered that scald reduced the yield of susceptible varieties by 15 per cent in some years. Sarasola and Campi (1947A) tested about 250 varieties of barley, and a considerable number of species of other genera for their reaction to Argentine races of the fungus. Several varieties were resistant to all cultures of the pathogen, which were considered to represent at least four physiologic races. Mackie (505) observed a very close approximation to a 3 : 1 ratio of segregating or homo-

zygous susceptible to homozygous resistant $F_3$ families. Riddle and Briggs (1950A) reported that in several varieties (La Mesita, Trebi, Turk and California No. 1311) there was one dominant gene for resistance to scald. In crosses with a susceptible variety, Atlas, monohybrid ratios were obtained for this dominant gene. Trebi and California 1311 appeared to have a recessive gene for resistance in addition to the dominant factor.

(70) Black or Semi-Loose Smut (*Ustilago nigra* Tapke).

The writer found no genetic studies on reaction to this disease.

(71) Covered Smut (*Ustilago hordei* (Pers.) Lagerh.).

Probably because of technical difficulties in obtaining successful inoculations (Tapke 1940A, Tapke and Bever 1942A), the genic basis of reaction to *U. hordei* has not been established (1, 413). Faris (217, 218) observed that various environmental factors (time of planting, temperature, type of soil, *etc.*) affected infection. Physiologic races of the pathogen, as well as varieties of the host differed in their response to the environmental factors (218). Broili (106) noted that some varieties were more susceptible to infection with *U. hordei* (and also *U. nuda*), and studied some of the conditions that affected establishment of the pathogen, but did not study the genetics of the reaction. Pugsley and Vines (642) obtained evidence that one variety, Kwan, had more than two dominant genes for resistance. Poehlman (619) tested the field reaction of about 250 varieties for several years, but did not study the genetics of difference observed. Yu et al. (1934A) inoculated seeds of 369 varieties with dry spores and found that 138 of the varieties were smut free in each of the eight years of the test.

(72) Loose Smut (*Ustilago nuda* (Jens.) Rostr.) (un—7; un2 — ; un3— ; un4— ; un5— ).

Studies on the genetics of reaction to *U. nuda* have been complicated by lack of reliable methods for infecting susceptible plants (681), but improved technics have been developed (Poehlman 1945A, Schaller 1949A, Shands and Schaller 1946A, Thren 1938A). Lasser (1938A) found that vernalized seeds were rarely diseased, so he concluded that vernalization should not be

used in breeding for resistance. In general, resistance appears to be dominant, or nearly so, and dependent on one gene in most crosses between resistant and susceptible varieties (495, 568, 693, 712, 855). In addition to, or possibly because of, unreliable methods of inoculation, modifying factors have been postulated as interfering with clear-cut segregations (495, 568).

Taylor and Harlan (802) observed that lateral florets of some varieties were more likely than central florets to develop seeds that gave rise to smutted plants. The lateral florets tended to stand open longer than the central florets, thus facilitating natural crossing and infection with smut.

Schaller (693, 1949A) found that resistance was controlled by one dominant gene in some crosses; but one incompletely dominant and one recessive gene were responsible in a cross between Brachytic, a smut resistant mutant in variety Himalaya, and Newal, a susceptible variety. In crosses between resistant varieties, susceptible $F_3$ lines were obtained, indicating that the varieties had different genes for resistance. From all the varieties and crosses tested, three genes for resistance were identified (un3, un4, un5), in addition to verifying one of the two genes for resistance previously reported by Livingston (495). Un3 was not linked with genes in Groups 1, 2, 3, 4 and 6 which were tested.

Nahmacher (568) found that resistance to two physiologic races of *U. nuda forma* sper. *hordei* was dominant and segregated in a 3:1 ratio in a cross between two varieties, but in other crosses dominance and segregation were not so clear.

Evidence of transgressive segregation in the direction of greater susceptibility and of increased resistance in crosses of resistant or moderately susceptible varieties has been obtained (681, 693, 910).

Shands (712) reported a close linkage between genes for resistance to stem rust and loose smut. Poehlman (617) found that most of the 23 hooded varieties tested were resistant, while most of the 42 awned varieties were susceptible, but the genetics of the correlation was not studied. Poehlman also determined the field reaction of over 200 varieties of winter barleys, mainly from the Orient and Eastern Europe, to both *U. nuda* (618, 619) and to *U. nigra* (619).

Histological methods for detecting loose smut in embryos were reported by Simmonds (717).

(72a) Snow Mold (Snow Rot) (*Typhula graminum* Karsten).

Little was found in the literature on this disease which is extremely destructive in areas where temperature and snow conditions are favorable for its development. Japanese workers Bokura (81) and Tasugi (1930A) have reported differences between varieties in their susceptibility to the pathogen. In one test (81) the percentage of injured plants ranged from 3 to 100 in different varieties.

(73) Barley Stripe or Stripe Disease (*Helminthosporium gramineum* Rabh.) (hg— ; hg2— ; hg3— ).

According to Christensen and Graham (1934A), there are a large number of biotypes of the stripe pathogen—possibly over 100. Isenbeck (1937A) found that the percentage of infection varied with the biotype, inoculation temperature, soaking temperature, and color of the light. Genau (1928A) noted that 66% of the small seeds developed striped plants as compared with 23% of the plants from large seeds. Kiessling (438) also observed that the small, apical seeds were more liable to infection. Varieties differed in susceptibility, and infection was strongly affected by environmental factors, particularly temperature. Seed treatments with $CuSO_4$, silver and mercury salts, reduced the number of diseased plants. Smolak (1926A) reported that stripe caused losses of 20–60% in Czechoslovakia, and that it could be controlled by seed treatments with certain chemical products, namely "germisan" and "uspulum". Suneson (1946A) showed that stripe could reduce the yield of susceptible types by as much as 50% in California. Environment has much to do with the development of the disease (710, 713).

Studies on the genic basis of resistance are apparently handicapped by difficulties in obtaining effective inoculations. Male sterility has proved helpful in this respect (766, Suneson 1950A). Usually resistance or immunity appears to be at least partially dominant (34, 278, 414, 912), but Suneson (1950A) and Suneson and Santoni (768) found almost all grades from dominance of resistance to dominance of susceptibility.

The number of genes involved in stripe reaction seemingly varies from one to three (34) or more (398, Suneson 1950A) in different varietal hybrids. Arny (35) found a second strain of the stripe-causing organism for which the reaction appeared to be

controlled by a single gene pair. There have been reports of transgressive segregation for increased susceptibility (398, 414).

Shands and Arny (1944A) found distinct differences in resistance to the stripe pathogen among 375 varieties tested, but no genetic tests were reported. Yu and Hwang (1935A) found that 62 of 184 varieties tested were infected by stripe inoculum. Thirty-nine varieties were resistant to both stripe and covered smut.

(74) Nematodes (*Heterodera schachtii* Schmidt).

Nilsson-Ehle (581) reported that immunity to nematodes was dominant and apparently controlled by a single factor difference. It was observed that resistance to nematodes was associated with high gramine content (93, 581). Whether or not gramine content was genetically controlled was not determined (93).

(75) Non-Parasitic Leaf Spots.

Christensen (131) reported that in some years non-parasitic leaf-spotting caused more damage to the barley crop in Minnesota than diseases caused by micro-organisms. The leaf spots were of various types—some closely resembling symptoms of disease organisms. Some types were found to be determined by heritable factors, while others seemed to result from malnutrition or toxic substances in the soil. Boron was the only substance, among 20 that were tested, that produced leaf-spotting. The number of genes responsible for susceptibility to spotting was not determined.

GENETICS OF MALTING VALUE. Since one of the chief uses of barley is as a subject for the brewer's art, it is natural that a good deal of attention has been devoted to malting quality and its genetic basis. It has long been recognized (53, 65, 68) that the percentage of nitrogen in the grain has a close connection with malting value. For that reason genetic studies on protein and/or nitrogen content are discussed, along with the limited studies on enzymes, under the heading Malting Value. However, other varietal characteristics that may also be heritable, such as carbohydrate characteristics (357), wort attenuation, viscosity, turbidity, diastatic activity and malt extract (19, 526), also affect malting value.

It has been reported that heredity has much less influence than environment on the "quality" (53) or protein content of malting barley (18, 330, 357). However, after a long series of studies on many varietal and environmental factors that affect the malting value of barleys, Anderson and co-workers (526) concluded that both types of factors are important. According to Anderson (18) and Harrison (330), varieties grown under identical conditions rarely differ by more than 1.5% in protein content, whereas the protein content of the same variety grown under widely different conditions may vary by as much as 10%. Seeds differing by as much as 8.2% in protein content, when grown together, produced crops with a range of only 1.7% in protein content (851). Beaven (53) found considerably greater differences in nitrogen content between years than between varieties, but concluded that nitrogen content was definitely genically determined, although he did not analyze its genic basis. Tedin (803) and Kiessling (437) also concluded that variety was of little importance as compared with environmental factors in determining protein content. Biffen (65) stated that there were actually differences in the protein content of grains in the same spike. Nelson (574) reported a correlation between the protein content of parents and bulked $F_2$ populations in crosses involving only one of four varieties crossed on 20 other varieties. The most important environmental factor affecting protein content of seeds was available soil moisture during the growing season, particularly in the early stages when vigorous vegetative growth was stimulated if moisture was abundant (18). Disease also affects protein content and other factors that determine quality (577). Fertilization, sunshine, temperature, stage of maturity at harvest (330) and date of seeding (223) are probably all more important than the variety in determining protein content.

Grant and McCalla (1949A) found a clear negative correlation between yield and protein content in barley and wheat. There was about a 0.05% decrease in protein content for each bushel increase in yield.

Barbacki (49, 50) found that in crosses between European and Himalayan barleys, the latter having higher grain nitrogen content, low nitrogen content was dominant. Studies of later generations up to $F_6$ showed a complicated genic basis for the character. There

seemed to be an association between higher N content and the factors for two rows and dark-colored naked kernels. There was not such a clear association between grain N content and time of shooting; length of straw, ears or awns; number of spikelets; spike density; or yield per plant. Reference was made by Barbacki to other reports on the genetics of nitrogen content which have not been available for perusal by the writer.

Observations by Freistedt (234) agree in a number of particulars with those of Barbacki. Among 250 varieties studied there was no distinct difference between spring and winter types with respect to protein content. However, some spring varieties from Japan contained as much as 6% more protein than German varieties. Protein content was considered to be a heritable character, but the genic basis was not determined.

Others likewise have had difficulty in analyzing the hereditary basis of protein content (360, 516, 837). Contrary to the findings of Barbacki (50), Tschermak (837) found high protein content was dominant to low protein content and apparently conditioned by several genes. Others have reported nitrogen content to be a heritable character (164, 437, 480) but determined by multiple factors (480, 516) and greatly influenced by environment (164). Transgressive segregation, resulting in higher nitrogen content in $F_3$ plants than in the parent varieties, was obtained by Lejeune (480).

Honecker (365) noted that partial sterility might increase the protein content from 10 to as much as 23%. In this case and according to Kiessling (437), increased protein content was associated with increased seed size. However, Kiessling suggested that since both protein content and seed size were genically determined, it should be possible to combine them in any desired combination. On the other hand, Kopecky (449) found no difference in the percentage of protein, moisture or ash between seeds of different sizes, e.g., seeds from different positions on the same spike.

Ivanov and Sarova (400) found that microscopic observations on albumen content may be useful in distinguishing malt and feed barleys, as well as between varieties. Malt types had lower albumen content than did feed barleys.

Only a few observations bearing on the genetics of enzyme content have been reported. Meredith et al. (527) noted that certain

varieties were high in activated diastatic power; but for the production of lines with high malt diastatic power these varieties were of no greater value as parents than were varieties which were low in diastatic capacity. Nelson (574), on the other hand, found a correlation between the diastatic power of parent varieties and bulked $F_2$ progenies. Catalase content of eight-day-old etiolated seedlings varied among varieties and with seasons (171). Northern varieties tended to have a higher concentration of the enzymes than did southern (Russian or European) varieties. Low catalase content seemed to be dominant.

Barley varieties also differ in the rate at which they absorb or give up moisture in the malting process; and in the type of product obtained by malting under different conditions of temperature, water hardness, etc. (162).

MATERNALLY INHERITED VARIANTS. Several maternally or cytoplasmically inherited mutants have been reported in barley. Most of these have been variegations (13, 32, 33, 382, 384, 385, 386, 738), but one was a more unusual self-colored type (664). Two of the variegated mutants seemed to be conditioned by both plastid inheritance and genes (32, 33, 385, 734). In one cross using pollen of variegated plants on normal plants, Arnason et al. (32) obtained one variegated among 42 $F_1$ plants. Usually, however, cytoplasmically determined characters are not transmitted through the pollen (384, 385, 664, 724). Robertson (664) tested a maternally inherited self-colored mutant with factors in each of the seven linkage groups and found no indication of linkage.

The extensive studies of Japanese workers on a variegated barley (382, 384, 385, 386, 734, 736, 738) were summarized by Imai (385). Plants homozygous for a gene for variegation gave rise to varying proportions of variegated, white and mosaic progeny. Typically variegated plants had fine white stripes in otherwise green leaves. Evidence indicated that a recessive gene, which was stable, stimulated plastids to mutate (irreversibly) from green to white and yellow to white. Plastid "exomutation", or mutation from green to white, was restricted to the early post-embryonic stage (382) and was affected by environmental factors, such as planting time. This was evident from the fact that the proportions of seedlings of different types was affected by time of planting (384).

In the later phases of the studies a white-variegated plant gave rise to a tricolored seedling with yellowish leaves having green and white stripes (385). This tricolored plant was considered to be the result of a plastid mutation from green to yellow. The green and white stripes were thought to result from mutations of the yellow plastids to green or white, respectively. The proportions of white-variegated, tricolored, yellow and white seedlings in the progeny depended on the proportions of these colors in the plants or spikes tested (385).

Imai (382) also briefly related finding a yellow-striped plant which produced yellow seedlings from the yellow part of a variegated ear, and only green seedlings from the green portions of the plant. Whether or not the striping was cytoplasmically inherited was not determined.

MEIOTIC IRREGULARITIES AND OTHER STERILITY VARIANTS. Ordinarily barley plants are highly fertile. Smith (725) found that about 92% of the florets on normal plants produced seeds. Müntzing (553) observed the percentage of "good" pollen in barley, as well as in plants of 16 other species, and found that of 59 plants, all but four had more than 90% "good" pollen. The four had 80–90% "good" pollen. Rye, among the other species observed, was particularly variable in pollen fertility. Failure to set seed may be a varietal characteristic, but it is affected by environmental factors, including date of seeding (541, 900).

Only a few mutants characterized by irregular meiosis have been reported in barley. Ekstrand (170) found a spontaneous, and Burnham (117) an x-ray-induced mutant for partial desynapsis. Reduced chiasma frequency, univalents, lagging chromosomes, micronuclei and other aberrations were frequent at micro-sporogenesis. Each of the two mutants was monofactorially controlled. The mutant found by Burnham was studied in considerable detail by McLennan (522). Pollen abortion averaged 22% and ovule sterility 48%, with the central florets having a greater reduction in seed set than did the laterals. The gene (1c) for the character seemed to be linked with n (Group 3).

Smith (726) described an unusual type of meiotic irregularity that had as its chief characteristic the assembling of large numbers of bivalents on one metaphase plate. Evidence indicated that in some cases chromosomes passed from one microsporocyte to

another, suggesting that the forces which caused chromosomes to assemble on metaphase plates in this mutant transcended the normal cell boundaries. In other instances the presence of quadrivalents indicated that the microsporocytes had formed a more or less plasmodium-like mass, allowing free movement of the chromosomes at an early stage of meiosis. The length of the spindle was independent of the breadth. The mutant was a monofactorial recessive. Swenson [15] tested the irregularity with genes in each of the seven linkage groups without finding evidence of linkage.

Gustafsson (297) reported that mutants affecting fertility were about as numerous in $X_2$ of x-rayed progenies as all types of chlorophyll mutants combined. However, no cytological analysis was made of the causes of the sterility. Vestergaard (860) noted six apparently normal but completely sterile plants in a population of 50 $F_2$ plants, but a progeny test of three of the normal plants failed to reveal any more of the sterile type.

Smith (725) examined eight mutant stocks, four of them characterized by partial or nearly complete sterility, and found meiotic disturbances in only one (726). Kattermann (430) also examined mutants exhibiting sterility without finding evidence of meiotic irregularity.

The writer [16] found about 50 cases of sterility of various degrees in $X_2$ of x-ray- and atomic-bomb-irradiated populations. No effort was made to compare the frequencies of seedling and sterility mutants, but the frequency of the latter seemed high.

Honecker (365) reported one particular mutant that had variable sterility averaging around 20% of the florets. The character was recessive and seemed to result from poorly functioning pollen. The sterility was associated with a factor for short awns. Other cases of genic sterility were observed, in some of which the degree of sterility varied with conditions. It was also noted that some varieties in some years had sterility amounting to as much as 20%, although in other years or under other conditions they were completely fertile.

Two male- or pollen-sterile mutants have been reported in barley (42, 764, and G. A. Wiebe, Unpub.). These mutants are both monofactorially determined recessives. Suneson and co-

[15] Unpublished information.

[16] Unpublished observations.

workers have carried on a number of experiments to determine the feasibility of using male sterility in the commercial production of hybrid seed (765, 767). Natural-crossing on male-sterile plants varied from year to year and with the homozygosity of the segregating populations (654), as well as the variety used as the pollen parent (764). The experiments are still in progress.

Suneson and Houston (766) and Suneson (1950A) found male-sterile plants useful in studies of susceptibility to floral infection. Spores of *Helminthosporium gramineum* and *Ustilago nuda* were tested.

Miche (530) analyzed some data of Johannssen (citation not obtained) in which there seemed to be three maxima of sterile florets at 0%, 50% and 75%. The observations were interpreted on the basis of three multiple alleles. Blaringhem (75) also reported variable sterility in a line of barley.

STUDIES ON HETEROZYGOTES. Under this heading will be discussed only certain special studies and unusual characters. Observations on the degrees of dominance of spike characters, earliness, etc. are indicated in the reviews of reports on the genetics of those characters.

A number of studies have dealt with the effect of apparently recessive genes in the heterozygous condition. Nilsson-Ehle (580) found that four homozygous normal plants had an average of 4.0 g., while 11 plants heterozygous for a gene for white seedlings averaged 3.4 g. The two classes were outwardly indistinguishable. Robertson (661, 662) and Robertson and Austin (667) studied genes for seedling (chlorophyll) lethals and reported that they had no measurable detrimental effect as single or double heterozygotes. One white-seedling factor was associated with an endosperm effect and did reduce the yield of grain per plant (662). However, not all chlorophyll-defective mutants are associated with visibly abnormal endosperms (662, 888).

Gustafsson (293, 296), studying the same sort of mutants (white and yellow seedlings) and the same quantitative characters studied by Robertson as well as seed longevity, reported that some monohybrids were superior to normal sister plants and that dihybrids exhibited additive heterosis. He also felt that the data of Robertson (662) and of Robertson and Austin (667) showed

heterosis of heterozygotes. In populations segregating for two lethals (*albina 7* and *xantha* 3) phenotypically normal plants of four different genotypes—AABB, AABb, AaBB, and AaBb—were tested for spike number, grain number and grain weight per plant. The ratios were 100:134:122:129; 100:128:120:127; and 100:134:126:133, respectively, from which it was concluded that the homozygous dominant class was "distinctly inferior" (300). Some other mutants were not effective in producing heterosis in the heterozygous condition. The observations on single and double heterozygotes were extended by Gustafsson and Nybom (1950A) to include treatments with high temperatures. Similar evidence of superior tolerance by the heterozygous seeds was obtained.

Euler and co-workers (187, 496) were unable to find any difference in the chlorophyll content of homozygous green plants and plants heterozygous for a white or yellow-green mutant. Euler (182) and Euler et al. (196, 207) were also unable to detect any difference in catalase activity between homozygous and heterozygous normal plants, although the catalase activity of the homozygous mutant (white seedling) was only half that of the other two classes. Likewise Nilsson-Ehle (585) was unable to find any difference in the oxygen consumption of homozygous normal plants and plants heterozygous for a white seedling character.

Tedin and Tedin (806) and Tedin (808) stated that there was some indication that plants heterozygous for the factor for two-rows vs. six-rows were taller than plants homozygous for either gene.

An interesting case of inviable varietal hybrids was reported by Wiebe (889). The inviability of $F_1$ plants of a cross between Manchuria and Deficiens was shown to be determined by complementary genes.

DOMINANT OR INCOMPLETELY DOMINANT VARIANTS. Only a few cases of partially dominant chlorophyll deficiencies have been reported. One of these was recorded by Kiessling (436, 439). The mutant was characterized by light green foliage and other characters. In $F_2$ there were 1 normal : 2 intermediate : 1 abnormal plant. R. G. Shands [17] also studied an incompletely dominant almost white character. Heterozygotes were yellow-green

[17] Unpublished observations.

and seemed to grow more slowly than homozygous normals. Homozygous mutant plants were inviable.

Cases of dominant or partially dominant morphological variants are somewhat more numerous. According to Harlan (314), hooded barley probably arose as a mutant something over 100 years ago. He found a sterile hooded plant in a breeding nursery, which he considered to be the result of another such dominant mutation. Ikeno (380) reported an *intermedium*-type that occurred in the $F_2$ of a cross between six-rowed varieties. It behaved as a dominant in crosses with six-rowed types. Gustafsson (286) obtained at least one partially dominant mutation for dense ears. A dominant dwarf was reported by Miyazawa (545); homozygous mutant plants were extreme sterile dwarfs.

A partially sterile, incompletely dominant, many-noded dwarf was reported by Honecker (365). The heterozygous plants were weak and deficient in numbers. They produced few seeds, which was interpreted as indicating that the homozygous "mutant" seeds aborted. Another mutant which was normal in appearance but partially sterile was similarly interpreted.

Huber (375) noted that one of five spikes on an $F_2$ plant of the cross, *H. distichum* × *H. spontaneum*, possessed pubescence, even on the awns. Progeny of the hairy spike did not exhibit the character, so it was surmised that the hairy condition resulted from a chimera that did not affect the sex organs.

ABERRANT SEGREGATIONS. Workers who have studied many genetic characters have noted that not all $F_2$ segregations are exactly 3:1, although only one gene pair is involved. There are a number of possible reasons for this discrepancy between theoretical and observed ratios. However, not many workers have taken the time and trouble to determine which of the possibilities actually obtain. Hallqvist (304) did take the trouble with a dwarf mutant which also affected chlorophyll development, and found that there was an elimination of gametes bearing the gene for the dwarf character. Among 26,000 $F_2$ plants, only 18% were dwarf, though germination of seeds from homozygous and heterozygous plants was practically identical and too high (98%) to account for the deficiency of dwarf progeny. Reciprocal crosses of normal and heterozygous plants revealed that the elimination resulted from a

reduction in transmission of the gene for dwarf through the pollen. In a later study (305) with 13 other mutants, none was found to differ significantly from a 3 : 1 $F_2$ ratio.

Chance fluctuations from theoretical ratios may be quite wide, however. Heinish (348) found a white-seedling mutant that segregated in approximately 3 : 1 ratio in the progeny in which it was first noted. In progeny tests of later generation heterozygotes the ratio ranged up to 152 : 2, although most of the ratios were approximately 3 : 1.

Moh (1950A) found in a study of atomic bomb- and x-ray-induced seedling mutants (731a) that over 20% of the heterozygous $X_2$ plants gave ratios of normal to mutant progeny that differed significantly from the theoretical 3 : 1. These aberrant (both high and low) ratios were characteristic of certain mutants. The average ratio for over 400 independent mutants was about 4 : 1 instead of 3 : 1.

The above observations and many others of investigators who have studied a goodly number of mutants in any species indicate the fallibility of drawing conclusions from limited data as to the number of genes responsible for the expression of a given character.

Honecker (365) observed a highly aberrant segregation in the progeny of an incompletely dominant many-noded-dwarf mutant. Heterozygous plants gave 0.4 normal : 1 lethal offspring. There was a considerable deficiency of heterozygous plants which were reduced in vigor and partially sterile. Another mutant, which was normal in appearance but partially sterile, gave 1 normal : 1.3 heterozygous progeny. No cytological observations were reported on either mutant.

Hara (309) likewise observed highly aberrant ratios of normal to white seedlings. A mutable-gene hypothesis was suggested.

Ikeno (380) obtained an *intermedium*-like mutant in a cross between two six-row varieties. The *intermedium* plants had the peculiarity that heterozygous plants frequently produced six-row and two-row tillers (381). The two kinds of spikes on the same plant were interpreted as resulting from somatic segregation.

Kiessling (440), in a study of a mutant white stripe, found that normal plants heterozygous for the striping factor gave rise to normal, striped and white progeny in varying proportions. Usu-

ally there was a deficiency of striped plus white plants for a ratio of 3 normal : 1 mutant.

Cytoplasmically controlled mutants have been reported to segregate in non-Mendelian ratios (cf. section on Maternally-Inherited Variants.).

## Linkage Studies

Most of the material for this section came from the recent and thorough summaries of linkage studies of Robertson et al. (676, 677). The writer tried to determine whether or not these summaries cited all references to papers dealing with linkage studies. If the citation was present in these authors' references, no further check was made as to whether or not data on a particular combination was given in the tables. If the reference was not present, an effort has been made to add the omitted linkage observations to the summaries. References to the original reports on linkage studies are given herewith in order to make the literature citations more complete.

The linkage data are summarized briefly in Figs. 1 to 8 in the Appendix.

*(To be Concluded in the May issue)*

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